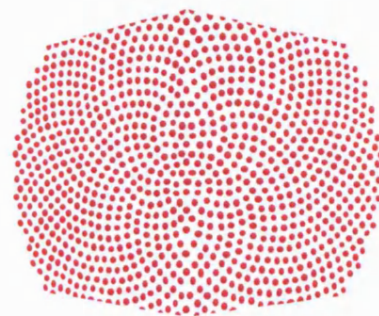


The Fate of Irrelevant Stimuli in Pavlovian Conditioning

Jemma Dopson

A thesis submitted for the degree of Doctor of Philosophy.



School of Psychology

UMI Number: U584606

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



UMI U584606

Published by ProQuest LLC 2013. Copyright in the Dissertation held by the Author.
Microform Edition © ProQuest LLC.

All rights reserved. This work is protected against
unauthorized copying under Title 17, United States Code.



ProQuest LLC
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106-1346

Declaration

This work has not previously been accepted in substance for any degree and is not concurrently submitted in candidature for any degree.

Signed..... (candidate) Date ...21/5/09...

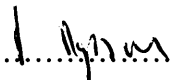
STATEMENT 1

This thesis is being submitted in partial fulfillment of the requirements for the degree of PhD.

Signed..... (candidate) Date ...21/5/09...

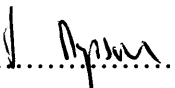
STATEMENT 2

This thesis is the result of my own independent work/investigation, except where otherwise stated. Other sources are acknowledged by explicit references.

Signed..... (candidate) Date ...21/5/09...

STATEMENT 3

I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

Signed..... (candidate) Date ...21/5/09...

Contents

Contents	i
Acknowledgements	iii
Summary	iv
1. General Introduction	1
The Rescorla-Wagner (1972) model	2
Mackintosh (1975a)	10
Pearce and Hall (1980)	19
The Comparator Hypothesis	26
Summary	33
2. Evaluation of the Rescorla-Wagner (1972) and Comparator Hypothesis Accounts of Blocking	35
Introduction	35
Experiment 1	38
Experiment 2	46
Experiment 3	52
General Discussion	61
3. The Role of Attention in Discrimination Learning	69
Introduction	69
Experiment 4	73
Experiment 5	89
General Discussion	105

4. Further Analysis of the Role of Attention in Discrimination Learning	110
Introduction	110
Experiment 6	115
5. Further Analysis of the Theory of Attention Proposed by Mackintosh (1975a) ...	130
Introduction	130
Experiment 7	139
6. General Discussion	162
Summary	162
Le Pelley (2004)	164
Pearce, George and Redhead (1998)	171
Future Directions	175
General Conclusions	181
References	182

Acknowledgements

I am very grateful to my supervisors, Prof. John Pearce and Dr. Dave George. Throughout my Ph.D. John has always been available to discuss my research and the details of associative theory, offering much needed support and encouragement when things didn't go according to plan. Dave has provided helpful advice, useful discussions and invaluable assistance with computer programming.

Thank you to Dr. Mark Haselgrove for his advice relating to the research presented in Chapter 2, and to Dr. Guillermo Ramos Esber, for his thorough introduction to conducting research with pigeons, and his support throughout my Ph.D.

Finally, I would like to thank the technical staff at the School of Psychology, particularly Dennis Simmonds, Denis Price and Rick Nash for building and maintaining the experimental equipment that I used for this research.

Summary

This thesis investigated the fate of irrelevant stimuli in Pavlovian conditioning. In Chapter 1, several theories of learning were evaluated with respect to findings related to blocking (Kamin, 1969) and the relative validity effect (Wagner, Logan, Haberlandt & Price 1968). The majority of these theories explain such effects by assuming that little is learned about irrelevant stimuli (e.g. Rescorla & Wagner, 1972; Mackintosh, 1975a; Pearce & Hall, 1980). In contrast, the comparator hypothesis (e.g. Miller and Matzel, 1988) makes the assumption that learning about irrelevant stimuli occurs, but is not expressed.

The three experiments reported in Chapter 2 tested this assumption using an extended version of the blocking procedure. In each case, an arrangement which, according to the comparator hypothesis, should cause a reversal of blocking failed to produce this result. The findings were, however, consistent with theories which assume that little is learned about irrelevant stimuli.

The experiments reported in Chapters 3, 4 and 5 were conducted to determine whether little is learned about these stimuli because animals do not attend to them (e.g. Mackintosh, 1975a; Pearce & Hall, 1980). Discrimination training designed to measure associability changes was given, using an autoshaping procedure with pigeons, and a Pavlovian conditioning procedure with rats. The results ruled out several non-attentional interpretations, and suggested that an attentional process was involved, which, rather than directing the eyes towards relevant stimuli and away from irrelevant stimuli, operated once all stimuli had been perceived. The results were consistent with the theory of attention proposed by Mackintosh, although it is acknowledged that this theory has its limitations. In the final chapter, two hybrid theories that overcome these limitations were discussed.

1. General Introduction

Animals are capable of learning about the relationship between stimuli that occur together in their environment, which enables them to behave adaptively. Such learning inevitably takes place against a background of other, irrelevant stimuli, the influence of which needs to be attenuated if the most useful associations are to be made. This thesis explores the fate of these irrelevant stimuli during the learning process. Two well-documented procedures in the animal learning literature that provide a useful starting point for this investigation are blocking and relative validity, which demonstrate convincingly that irrelevant stimuli participate less in associative learning than relevant stimuli.

During the standard blocking procedure, subjects receive pairings of a stimulus, A, with an outcome before reinforced trials of A in compound with a novel cue, X. Subsequent responding to X alone is found to be reduced relative to that observed in a group that did not receive the initial conditioning with A (e.g. Kamin, 1969). Thus pretraining with A is said to block learning about X, a stimulus whose presence is irrelevant to the delivery of the outcome. The relative validity effect was first demonstrated in an experiment by Wagner, Logan, Haberlandt and Price (1968). One group of rats received a true discrimination, in which reinforced presentations of the compound AX and nonreinforced presentations of the compound BX were presented. Another group received a pseudo discrimination, in which presentations of both AX and BX were reinforced on 50% of their presentations, and nonreinforced on the remaining trials. This training was followed by test trials on which X was presented alone. It might be expected that responding to X would be comparable in the two groups as this stimulus signalled reward on 50% of trials in both cases. However, Wagner et al. found that the pseudo discrimination group demonstrated

more conditioned responding in the presence of X than did the true discrimination group. Thus X had more control over behaviour in the pseudo discrimination group, when it had been accompanied by stimuli that were equally relevant to the outcome, than in the true discrimination group, when it was irrelevant to the outcome.

I shall begin by reviewing the most influential explanation for these effects, the Rescorla-Wagner (1972) model. Despite its successes, this theory has been challenged by a number of findings related to blocking and relative validity. Therefore I shall also evaluate alternative theories with respect to these results, with the aim of finding the most effective explanation for the fate of irrelevant stimuli.

The Rescorla-Wagner (1972) model

According to the Rescorla-Wagner (1972) model, stimuli compete for a limited pool of associative strength in order to acquire control over behaviour, and changes in the associative strength of a stimulus (ΔV_A) are determined by Equation 1.1.

$$\Delta V_A = \alpha\beta(\lambda - V) \quad (1.1)$$

In this equation, α and β represent the salience of a conditioned and unconditioned stimulus (CS and US) respectively, and V the aggregate associative strength of all stimuli present on a given trial. λ represents the maximum associative strength that the US, or outcome, is able to support on a given trial ($\lambda > 0$ for a presented outcome, and 0 when the outcome is absent). Thus changes in the associative strength of a cue A (ΔV_A) on a given trial are proportional to the discrepancy between the outcome presented and that expected based on the cues present on that trial ($\lambda - V$).

The Rescorla-Wagner (1972) theory explains blocking by assuming that during its initial pairings with the US, A acquires considerable associative strength. Therefore the result of this training is that V is already high when X is presented in compound with A, leaving little associative strength to be gained by X during this stage of training. In this way, A is said to 'block' learning about X. The Rescorla-Wagner model is also able to account for the relative validity effect reported by Wagner et al. (1968). On the initial AX+ trial of the true discrimination, the associative strength of both A and X will increase comparably. Following a nonreinforced BX trial however, X will lose some associative strength. As A is consistently reinforced, this stimulus will eventually acquire a large proportion of the associative strength available, allowing relatively little to be gained by X. During the pseudo discrimination neither A nor B is consistently paired with the US, and thus neither of these stimuli is able to reduce the amount of associative strength gained by X to the same extent as A can in the true discrimination. Rescorla and Wagner acknowledge that this prediction is realised only if it is assumed that the learning rate parameter (β) associated with reinforcement is greater than that associated with nonreinforcement.

Several findings related to blocking have challenged Rescorla and Wagner's (1972) account. One set of findings concerns the role that surprise plays in the disruption of blocking. Kamin (1969) reported that if the intensity of the US used to condition A was increased for subsequent compound conditioning (AX+) trials, X elicited a notable conditioned response on test. The Rescorla-Wagner model accounts for this finding by assuming that presenting a stronger US during compound conditioning means that the value of λ during this stage is higher than it was during the initial conditioning with A. This increase in the value of λ allows associative strength to accrue to both A and X, with the result that conditioned responding will be

observed to X on test. Dickinson, Hall and Mackintosh (1976) replicated Kamin's finding, demonstrating that if each presentation of A during pretraining was followed by a single shock, but each presentation of the compound AX was paired with two shocks, blocking was attenuated when X was then tested alone. Problematic for the Rescorla-Wagner model however was the discovery that a comparable effect was observed when pretraining trials with A were followed by two shocks, and compound conditioning with AX trials were followed by just one. That is, the omission of an expected US produced just as much 'unblocking' as the presentation of an additional US. According to the Rescorla-Wagner model, rather than allowing excitatory conditioning to proceed to X, such an arrangement should promote inhibitory learning about X.

Although this unblocking result seems to be a significant problem for the Rescorla-Wagner model (1972), evidence for the formation of within-compound associations (e.g. Rescorla & Durlach, 1981) provides the model with an alternative interpretation of the effect. Rescorla and Colwill (1983) suggested that unblocking following the omission of an expected reinforcer could depend on the X-A association established during compound conditioning rather than on the X-US association formed during this stage. If this were the case, then if A is initially followed by two shocks, the X-A association formed during compound conditioning is between X and a more aversive A than when A is followed initially by just one shock. X will activate a representation of A on test, and via the stronger A-US association, notable conditioned responding will be elicited by X. If this explanation is correct, reducing the strength of the X-A association should reduce the magnitude of unblocking. Accordingly, Rescorla and Colwill found that unblocking was eliminated if the X-A association was reduced by extinguishing A alone, or by separate reinforced presentations of A after compound conditioning but prior to the test with X. Thus

Rescorla and Colwill provided evidence that unblocking following the omission of an expected reinforcer may not be as incompatible with the Rescorla-Wagner model as first thought. However, they also acknowledged that within-compound associations may not fully account for the effect.

Indeed, an appetitive procedure by Holland (1985) provides evidence against this account, the design of which is presented in Table 1.1.

Table 1.1. Design of the Experiment by Holland (1985).

Group	Stage 1	Stage 2	Stage 3	Test
Up-Shift Control	A+		AX++	X-
Down-Shift Control	A++		AX+	X-
Up-Shift	A+	AX+	AX++	X-
Down-Shift	A++	AX++	AX+	X-

In this experiment, initial presentations of A were followed by a reinforcer with a low value or a high value for groups up-shift control and down-shift control respectively. The low value reinforcer comprised the delivery of a single food pellet, and the high value reinforcer comprised the delivery of one pellet, followed by two more pellets five seconds later. During subsequent compound training, presentations of AX were paired with the reinforcer that had not been trained with A, so this constituted an upward shift in reinforcer value for half of the rats (low to high) and a downward shift for the other half (high to low). In both cases, considerable conditioned responding was observed on a subsequent test of X by itself, that is, an unblocking effect. However, if the compound was paired with the initial reinforcer before there was a shift in the reinforcer value, as in groups up-shift and down-shift, the unblocking effect on test was substantially reduced relative to when this phase was omitted. Including additional compound trials should increase the A-X association,

which according to Rescorla and Colwill (1983) should increase the unblocking effect. However, less unblocking was seen than when these additional trials were omitted.

Holland and Fox (2003) provided further evidence for the inadequacy of the Rescorla-Wagner (1972) account of blocking. The design of their experiment is presented in Table 1.2. For two blocking groups, a test with X alone after the standard blocking treatment was followed by either excitatory conditioning with X in group Blocking-E, or training known to promote inhibitory learning about X in group Blocking-I. According to the Rescorla-Wagner model, B+ BX- training endows B with positive associative strength. As λ is zero in the absence of the outcome, the error term will be negative on BX- trials and inhibition will be established to X. Half of the animals within each group had hippocampal lesions, and half had sham surgery.

Table 1.2. Design of the Experiment by Holland and Fox (2003).

Group	Stage 1	Stage 2	Test 1	Test 2	
Blocking-E	A+	AX+	X-	X+	
Blocking-I	A+	AX+	X-	B+	BX-

Holland and Fox (2003) found that the lesioned animals showed no difference to the sham-operated animals during Stages 1 and 2 and on the first test of X, during which the blocking groups showed comparably less responding to X than a control group which did not receive the initial conditioning trials with A. According to the Rescorla-Wagner (1972) model, conditioning of X should proceed readily during Test 2 for group Blocking-E because, owing to the low associative strength established to X following blocking, the discrepancy $\lambda - V$ is large. For group Blocking-I, inhibitory conditioning with X should also progress rapidly because of the low associative

strength of X. Holland and Fox observed that the lesioned animals in groups Blocking-E and Blocking-I acquired excitatory and inhibitory conditioning to X (respectively) more rapidly than sham-operated animals in the same group.

The failure of the sham-operated animals to learn readily about X following blocking suggests that as a result of the blocking treatment, X had become a less effective CS for these animals, rendering it unable to enter into associations with the US. In the lesioned rats on the other hand, X had somehow maintained its efficacy. This finding prompted Holland and Fox (2003) to suggest that although blocking may primarily be determined by the amount of associative strength that the US can support (λ), processing of the CS also seems to be affected. This idea is not compatible with the assumptions of the Rescorla-Wagner model (1972). A similar explanation can account for the slower rate of inhibitory conditioning with X in the sham than the lesioned animals in group Blocking-I.

Also problematic for the Rescorla-Wagner (1972) model is the finding that responding to X following blocking can increase without further training of X. According to this theory, because blocking is due to a failure of X to acquire an association with the US, responding to X should not increase without further presentations of X with the US. A blocking group in an experiment by Blaisdell, Gunther and Miller (1999) received pairings of A and a footshock prior to conditioning with AX before 800 nonreinforced trials with A were given. This treatment resulted in a reversal of the blocking effect such that on a subsequent test of X, greater conditioned suppression to X was evident in this group than in a second blocking group that received the same blocking treatment but exposure to the context rather than extinction trials with A.

Thus certain findings have proved to be problematic for the Rescorla-Wagner (1972) account of blocking. In addition, their interpretation of relative validity has

been challenged by Murphy, Baker and Fouquet (2001). The design of Murphy et al.'s experiments is presented in Table 1.3, which included a third stimulus, C, in the relative validity procedure.

Table 1.3. Design of Experiments 1 and 2 from Murphy, Baker and Fouquet (2001).

Group	Training		
True Discrimination 1 (TD1)	AX-	BX-	2 CX+
True Discrimination 2 (TD2)	AX+	BX+	2 CX-
Pseudo Discrimination (PD)	AX+/-	BX+/-	2 CX+/-

In Murphy et al.'s (2001) experiments there were two true discrimination groups. For one, TD1, AX and BX were both nonreinforced and CX was reinforced. For the other, TD2, AX and BX were both reinforced and CX was nonreinforced. Twice as many CX trials as AX or BX trials were given to both groups in order to ensure that X was reinforced on 50% of its presentations. In a pseudo discrimination group, PD, the trial types AX, BX and CX were each followed by reinforcement on 50% of their presentations. In one experiment, Pavlovian conditioning was used, and in a second experiment instrumental conditioning was used. Murphy et al. reported that in both experiments groups TD1 and TD2 responded to X at a comparable level, and that this was significantly lower than the responding observed to X in group PD.

This finding is at odds with the Rescorla-Wagner model (1972), which predicts that X should acquire more associative strength in group TD2 than in group TD1. In group TD1, C is consistently paired with the outcome on twice as many trials as either A or B is in group TD2. In group TD1, C will therefore gain more associative strength than either A or B in group TD2 and block the learning of an association between X and the US to a greater extent than either A or B can in group

TD2. As a result, X will have greater associative strength in group TD2, and more responding would be expected to this stimulus on test than in group TD1. There will then be a smaller difference between the level of responding observed to X in groups TD2 and PD than between groups TD1 and PD, and hence a smaller relative validity effect is predicted between groups TD2 and PD than between groups TD1 and PD.

The Rescorla-Wagner model (1972) also has difficulty accounting for the results of intradimensional and extradimensional shift (IDS/EDS) experiments, which involve true discriminations such as those given in the relative validity procedure. An example of one such experiment is provided by Mackintosh and Little (1969). A simplified version of their design is presented in Table 1.4. In this experiment, pigeons first received a discrimination in which two coloured stripes (A and B) were presented in two different orientations (W and X). For the IDS group, colour A reliably signalled food and colour B reliably signalled the absence of food. Both stimuli were therefore relevant to the outcome that followed them. The orientations W and X were both followed by food on 50% of their presentations and were therefore irrelevant. For the EDS group, orientations W and X were relevant, consistently signalling reinforcement and nonreinforcement respectively. Colours A and B were followed by food on 50% of their presentations and were therefore irrelevant. Following this training, both groups were transferred to another discrimination, in which two novel colours, C and D, and two novel orientations, Y and Z, were presented. For all animals, C and D were relevant to the delivery of food, and Y and Z were irrelevant. This discrimination constituted an intradimensional shift for group IDS as C and D, which were relevant during the test discrimination, were from the same dimension as A and B, which were relevant during training. In contrast, the test discrimination constituted an extradimensional shift for group EDS, as C and D were from a different dimension to the stimuli that were relevant for this group during

training (W and X). Mackintosh and Little observed that the IDS group acquired the test discrimination more readily than the EDS group. An explanation for this finding does not follow readily from the Rescorla-Wagner (1972) model, which would predict that the discrimination would be acquired at the same rate in the two groups as for all animals, each of the stimuli presented on test is novel.

Table 1.4. Simplified Design of the Experiment by Mackintosh and Little (1969).

Training				Test	
IDS group		EDS group		Both groups	
AW+	BW-	AW+	AX-	CY+	DY-
AX+	BX-	BW+	BX-	CZ+	DZ-

Many of the challenges to the Rescorla-Wagner (1972) model that have been discussed can be overcome if it is assumed that during discrimination learning animals pay more attention to stimuli that are relevant than to stimuli that are irrelevant. Of the theories that have been developed to explain how such changes in attention might occur, those proposed by Mackintosh (1975a) and Pearce and Hall (1980) successfully account for many of the weaknesses that have been identified with the Rescorla-Wagner model (1972). I shall begin with Mackintosh's theory.

Mackintosh (1975a)

According to Mackintosh (1975a), the rate of conditioning to a stimulus is determined both by a general learning rate parameter, θ , and by a stimulus-specific learning rate parameter, α , that represents the attention paid to the stimulus, or in Mackintosh's terms, the associability of that stimulus (see Equation 1.2).

$$\Delta V_A = \alpha_A \theta (\lambda - V_A) \quad (1.2)$$

A key difference between this proposal and that of Rescorla and Wagner (1972) is that changes in associative strength are determined by the discrepancy between λ and the associative strength of a given stimulus, rather than between λ and the sum of the associative strengths of all stimuli present on that trial. Another critical difference is that although the value of α is initially determined by the characteristics of the stimulus it corresponds to, in Mackintosh's model, it may vary with experience as a consequence of its correlation with reinforcement. That is, α will increase when a stimulus is correlated with reinforcement and decrease when a stimulus is uncorrelated with reinforcement.

The extent to which a subject learns to attend to or to ignore a stimulus depends on whether it is uniquely successful in predicting the outcome that follows it. Mackintosh (1975a) states that attention to cue A will increase if it predicts the outcome better than any of the other stimuli present on that trial, but will decrease if it is a less accurate predictor of the outcome than the other stimuli present. Such changes in attention to A are updated according to Equations 1.3 and 1.4 after each trial on which A is presented. V_X represents the associative strength of all other stimuli that were presented with A on that trial.

$$\Delta \alpha_A \text{ is positive if } |\lambda - V_A| < |\lambda - V_X| \quad (1.3)$$

$$\Delta \alpha_A \text{ is negative if } |\lambda - V_A| \geq |\lambda - V_X| \quad (1.4)$$

According to Equation 1.3, increases in the associability of A are expected if the discrepancy between the total associative strength that the reinforcer can support (λ) and the current associative strength of A (V_A) is smaller than that between λ and

the associative strength of all other stimuli present on that trial (V_X). Likewise, decreases in the associability of A are expected if the discrepancy between λ and V_A is greater than that between λ and V_X (Equation 1.4) Thus, whereas Rescorla and Wagner (1972) assume that the pairing of A with the US will increase the associative strength of A if the US is not otherwise predicted, Mackintosh (1975a) assumes that the pairing of A with the US will increase the probability of attending to A if the US is not otherwise predicted.

Mackintosh's (1975a) theory readily accounts for blocking. The initial training with A establishes it as a good predictor of the outcome. When X is then conditioned in compound with A, it is a poorer predictor of the outcome than A, meaning that its associability will decline over the course of compound conditioning. In a control group that does not receive the initial conditioning with A, A and X are equally good predictors of the outcome during compound conditioning, and the associability of X will be relatively higher in this group than in the blocking group. The difference between these two groups will only be apparent from trial two however, as the associability of X is adjusted only after its first conditioning trial. Mackintosh (1975b) found support for this prediction from a series of experiments. When rats received eight pairings of A with a shock followed by eight compound conditioning trials with AX, blocking was observed on a subsequent test of X alone. However, no blocking was observed when rats had received eight pairings of A with a shock before a single compound conditioning trial with AX.

In contrast to these findings, Balaz, Kasprow and Miller (1982) suggested that Mackintosh's (1975b) failure to observe blocking after a single compound conditioning trial could be due to an association established between A and X on that trial. This association might allow X to activate a representation of the US on test due to the strong A-US association established during training. The design of the

experiment reported by Balaz et al. was similar to that of Mackintosh (1975b), but each CS was presented for just five seconds, compared to the 25 seconds or 60 seconds used by Mackintosh. Such a measure was expected to minimise the A-X association formed during the compound conditioning trial, which should prevent X from activating a representation of the US on test. Sure enough, under these conditions, blocking of X was observed after pretraining of A was followed by a single AX+ trial. Further evidence of this effect was provided by Dickinson, Nicholas and Mackintosh (1983), who presented a blocking group with reinforced presentations of A, followed by a compound conditioning trial on which X preceded A by 5 seconds. Inserting a trace interval between X and A was expected to reduce the within-compound association between these two stimuli, and hence reduce the conditioned response to X on test. In line with this prediction, the blocking group demonstrated less conditioned responding to X than did a control group that had not received initial conditioning with A.

Despite this challenge to Mackintosh's (1975a) account of blocking, the theory can account for the results of Dickinson et al. (1976), which showed that the omission of an expected US during compound conditioning caused unblocking of X. According to Mackintosh, attention to A will increase during initial training when it is paired with two shocks as it is an accurate predictor of this outcome. However, when AX is then conditioned and the second shock omitted, the extent to which A can be regarded as an accurate predictor of the outcome is reduced. This arrangement therefore allows attention to X to be maintained at a sufficiently high level for it to gain considerable associative strength, which in turns allows X to elicit conditioned responding on a subsequent test.

The theory of Mackintosh (1975a) can also explain Holland's (1985) finding that if AX is presented with the same US initially trained with A, before being trained

with a US that is higher or lower in value, unblocking is reduced (see also Mackintosh and Turner, 1971). It follows from this theory that pairing AX with a US that had previously been trained with A will reduce the associability of X, as A has already been established as a consistent predictor of that US. Consequently, the associability of X at the beginning of compound training with the new upshifted or downshifted reinforcer will be lower than if X was novel at this point. As a result, little will be learnt about X and a small conditioned response will be evident on test.

Holland and Fox's (2003) finding that rats with hippocampal lesions learnt about X more readily than sham-operated rats after blocking can also be explained by Mackintosh's (1975a) theory. Holland and Fox link the loss of attention to relatively uninformative stimuli such as X to hippocampal system function (see also Baxter, Gallagher & Holland, 1999; Kaye and Pearce, 1987), and suggest that in normal rats blocking produces a loss of attention to X, but hippocampal lesions interfere with this loss. If X does not lose associability, then animals will learn readily about this stimulus. However, Holland and Fox's finding of a comparable blocking effect in the hippocampal and sham-operated animals, along with the results of Balaz et al. (1982), suggests that a reduction in the associability of X is not the only cause of blocking.

Holland and Kenmuir (2005) reached a similar conclusion, suggesting that when an expected reinforcer is omitted during compound conditioning, unblocking is the result of enhanced processing of the remaining US rather than enhanced processing of X. The design of one of their experiments, which provided evidence for this suggestion, is presented in Table 1.5. During Stage 1, two groups received presentations of A followed first by food and then five seconds later by sucrose, and presentations of B followed by sucrose. In a second stage, rather than presenting a compound of AX, A alone was again presented. For group downshift, each of these trials was followed by food alone, and for the control group trials with A were again

followed by food and sucrose. At test, presentations of X were followed by food and then sucrose for both groups, and the acquisition of conditioning to X was assessed. Greater conditioned responding to X was demonstrated in the downshift group than in the control group, a result analogous to the unblocking effect. Consistent with research by Holland and Gallagher (1993a), no such effect was observed for animals that had lesions to the central nucleus of the amygdala, suggesting that this region is critical to enhancements in learning rate when an expected event is omitted.

Table 1.5. Design of the Experiment by Holland and Kenmuir (2005)

Group	Stage 1	Stage 2	Test
Downshift	A → Food → Sucrose	A → Food	X → Food → Sucrose
	B → Sucrose		
Control	A → Food → Sucrose	A → Food → Sucrose	X → Food → Sucrose
	B → Sucrose		

Holland and Kenmuir's (2005) result is problematic for Mackintosh (1975a). The fact that enhanced responding to X can be observed even if it is never paired with A suggests that unblocking observed after an expected reinforcer has been omitted is caused by a change in processing of the remaining US, rather than by a change in the attention paid to X. In an attempt to reconcile their findings with those from studies that have found evidence for changes in CS processing, Holland and Kenmuir suggested that the processing of any event, CS or US, can be enhanced when surprise is induced by the omission of an expected reinforcer. There is however, an alternative interpretation of their result. In the control group, food was consistently followed by sucrose during both stages of training and on test. Such an arrangement could result in these animals forming a particularly strong association between food and sucrose. Thus it could be that when food follows X on test, a stronger representation of sucrose

is activated in this group than in the downshift group, which has just received A followed by food alone during Stage 2. If this were the case, then the control group might be more likely to approach the sucrose cup than the downshift group. In Holland and Kenmuir's experiment, the food and sucrose cups were located at different ends of the conditioning chamber, and so it could be that the short durations spent in both the food cup and the sucrose cup by the control group reflected the increased amount of time that this group spent travelling between them.

Taking these points into consideration, it seems that Holland and Kenmuir's (2005) result may not present an insurmountable problem for the Mackintosh (1975a) model. However, Blaisdell et al.'s (1999) finding that responding to a blocked CS, X, recovered after the blocking cue, A, was extinguished is problematic for Mackintosh. Like the Rescorla-Wagner model (1972), Mackintosh's theory does not anticipate that extinguishing A will influence subsequent responding to X. The low associability of X that resulted from its training in compound with A, which is already an accurate predictor of the US, should be maintained regardless of any subsequent treatment given to A in the absence of X.

Although Mackintosh's (1975a) account of blocking has been criticised, the model provides an appealingly simple explanation for relative validity. In the true discrimination group (AX+ BX-), the relevant cues A and B are the best predictors of reinforcement and nonreinforcement respectively. As the irrelevant cue X is not the best predictor of either outcome, its associability will decrease over the course of training, with the result that little responding to this cue will be evident when it is presented at test. In the pseudo discrimination group (AX+/- BX+/-), A, B and X are all equally relevant and thus equally good predictors of the outcome. Thus, over the course of training the associability of X will not decline to the same extent as in the

true discrimination group, with the result that on test relatively more responding will be evident to X in the pseudo discrimination group.

This explanation can also be applied to the results of Murphy et al. (2001). For the discrimination received by group TD1 (AX- BX- 2CX+, see Table 1.3), C is the best predictor of reinforcement, and A and B are both the best predictors of nonreinforcement. For the discrimination received by group TD2 (AX+ BX+ 2CX-), A and B are the best predictors of reinforcement and C is the best predictor of nonreinforcement. The associability of X is therefore expected to be comparably low in both groups by the end of training. Group PD received the discrimination AX+/- BX+/- 2CX+/-, for which all stimuli are equally predictive of the outcome. As a result, X will have more associability in this group than in groups TD1 and TD2, and relatively more responding should be evident to X on test than in the other groups.

Similarly, the results of IDS/EDS experiments can be interpreted easily if it is assumed that attention increases to stimuli that are relevant to the discrimination because they are the best predictors of the outcome. Consider the discrimination AW+ BW- AX+ BX- (Table 1.4) in which the colours A and B are relevant. Attention to both of these stimuli should increase, as A and B are the best predictors of reinforcement and nonreinforcement respectively. Mackintosh (1975a) proposed that changes in associability generalise to similar stimuli. As stimuli from the same dimension are likely to be more similar to one another than stimuli from different dimensions, increases in attention to relevant stimuli in the IDS group should generalise to stimuli that are relevant on the test discrimination, facilitating learning about these stimuli. In contrast, attention to orientation should increase during training in the EDS group, meaning that when transferred to the test discrimination this group will be at a disadvantage relative to the IDS group, as they have learned to attend to stimuli from a dimension that is now irrelevant.

Although Mackintosh's (1975a) theory appears to offer a simple explanation for these results, its assumption that increments in associative strength are established to individual elements presents a problem here. Such an assumption prevents inhibitory learning, and in doing so, leads to the prediction that the initial discrimination will never be solved completely. Consider the trial types AW+ BW-. B is consistently followed by nonreinforcement, and hence from the outset of training will have no associative strength. Although W will suffer a reduction in associability as training progresses, it will gain some associative strength through its pairings with the outcome. Thus by the end of training the overall associative strength of the BW compound will be positive, and responding to this compound will not have completely extinguished. In the final chapter I shall discuss how the theory proposed by Mackintosh has been adapted in order to take account of this issue.

Mackintosh (1974, p597) described the IDS/EDS effect as providing "perhaps the best evidence that transfer between discrimination problems may be partly based on increases in attention". Indeed, the effect has been observed by a number of researchers and in a number of species. As well as Mackintosh and Little's (1969) demonstration of the effect in pigeons (see also George and Pearce, 1999), the effect has also been reported in rats (Shepp & Eimas, 1964) and in marmosets (e.g. Dias, Robbins & Roberts, 1996). However, it must be noted that this effect is not always found. Hall and Channell (1985) reported three experiments conducted with pigeons, all of which used very similar procedures and stimuli to those used by Mackintosh and Little. Thus one group of animals was trained with a discrimination for which colour was relevant and orientation was irrelevant, and another group was trained with a discrimination for which orientation was relevant and colour was irrelevant. Both groups then received one test discrimination for which two novel stimuli from the initially relevant dimension were again relevant (IDS) and another test discrimination

for which two novel stimuli from the initially irrelevant dimension were relevant (EDS). At test, the discrimination for which colour was relevant was acquired more readily than that for which orientation was relevant, but the EDS discrimination was acquired at a comparable rate to the IDS discrimination in both cases (see also Couvillon, Tennant & Bitterman, 1976; Sutherland and Andelman, 1969).

One reason for the inconsistent results reported could be the use of novel stimuli during the test discrimination. Mackintosh's (1975a) explanation for the IDS/EDS effect is based on the assumption that associability generalises from one stimulus to another as a function of the similarity between the two. Although the implication of this assumption is that there will be greater generalisation from two previously trained colours to two novel colours as opposed to two novel orientations, the similarity of training and test stimuli that belong to the same dimension is also important. For example, if stimuli that were relevant during training were from a different end of the colour spectrum to those presented on test, a smaller IDS effect might be expected than if the colours from both discriminations were from similar positions along the spectrum. This analysis could explain why no difference is observed between the rate at which the IDS and EDS discriminations are acquired in some experiments, and suggests that a novel design for assessing attentional changes to irrelevant and relevant stimuli is required.

Pearce and Hall (1980)

Mackintosh's (1975a) model provides parsimonious explanations for some of the effects that the Rescorla-Wagner model (1972) fails to anticipate, justifying the suggestion that animals learn to attend to stimuli that are relevant at the expense of those that are irrelevant. However, Pearce and Hall (1980) questioned the mechanism that Mackintosh proposed was responsible for these changes in attention. The

fundamental assumption made by Pearce and Hall is that a CS will lose associability when it accurately predicts the US, precisely the circumstances which Mackintosh would argue lead to an increase in associability.

The Pearce-Hall (1980) model does not simply apply the opposite mechanism to that described by Mackintosh (1975a). As conveyed in Equation 1.5, according to the Pearce-Hall model, the associability of a stimulus (A) on a given trial (n) is determined by the discrepancy between the intensity of the US on the previous trial (λ^{n-1}) and the total associative strength of all stimuli that were present on that trial (V_T^{n-1}). According to Pearce and Hall then, at the beginning of conditioning with A, this error term will be large as A has little associative strength and the US is surprising, and the associability of A will be high. As conditioning with A proceeds and A gains an increasing amount of associative strength, the US will become less surprising, and the associability of A will decline.

$$\alpha_A^n = |\lambda^{n-1} - V_T^{n-1}| \quad (1.5)$$

Changes in the associative strength of A depend on its intensity (S), its associability (α) and the intensity of the US (λ), so that the change in the associative strength of A on trial n is determined according to the following equation

$$\Delta V_A^n = S_A \alpha^n \lambda^n \quad (1.6)$$

According to Equation 1.6, unlike the theories discussed thus far, the effectiveness of the US does not change as conditioning proceeds, and conditioning is determined solely by changes in CS effectiveness. When the associability of A is high, there will be a large increment in the associative strength of A on the next trial. As conditioning

with A progresses, the associability of A will decrease as A comes to accurately predict the outcome, and increasingly less associative strength will accrue to A.

The Pearce-Hall model (1980) accounts for blocking in the following way. When A is initially conditioned alone, its initially high associability will decline over the course of training as A consistently predicts the outcome. On the first trial on which X is presented in compound with A, the associability of X is determined by its own properties. Therefore, like Mackintosh (1975a), Pearce and Hall predict that learning about X will occur on this trial because it is novel and thus has high associability. However, on the second trial, the associability of X will be determined by the aggregate associative strength of A and X. This value will be close to λ due to the previous conditioning with A. As a result, the associability of both A and X will be low on this trial and little will be learned about X on this trial and subsequent trials.

The model can also explain Dickinson et al.'s (1976) finding that the omission of an expected reinforcer during the blocking treatment causes 'unblocking'. Over the course of pretraining, when A is paired with two shocks, its associability will decline as it is an accurate predictor of this outcome. On the first trial on which the compound AX is followed by just one shock, the associability of X will be determined by its own properties and associative strength will accrue to this stimulus. On the second trial, the value of λ determining the associability of both A and X will represent one shock, and thus will be smaller than for the first trial. The discrepancy $|\lambda^{n-1} - V_T^{n-1}|$ will therefore be greater than if the outcome had remained the same. As a result, the associability of both A and X will be maintained, allowing more associative strength to accrue to X relative to a control group that receives the same outcome during both stages.

The model is also able to account for relative validity. During true discrimination training, A and B accurately predict the outcome on AX+ and BX- trials respectively. As a result, the associability of these stimuli will decrease as

training progresses, as will the associability of X, which accompanies these stimuli. In contrast, during pseudo discrimination training (AX+/- BX+/-), neither compound is a perfect predictor of the outcome, and the associability of A, B and X will not decline to the same extent in this group as in the true discrimination group. These differences in associability allow the model to account for relative validity in the following way. In the true discrimination group, on the first few trials with AX+, A will gain associative strength as it accurately predicts reinforcement. As A gains associative strength, the compound AX will become progressively a more accurate predictor of the US, and the associability of both A and X will be forced towards zero. Although X may gain some associative strength on these initial AX+ trials, it is also present on BX- trials. On the first of these BX- trials, the associative strength of both B and X will be zero. From the first trial therefore, these stimuli accurately predict the outcome (nonreinforcement) and hence neither will gain much associability or associative strength. Thus, by the end of training, X will have low associative strength, and so will A and B. In the pseudo discrimination group, BX trials are followed by both reinforcement and nonreinforcement, and hence at the onset of training, these stimuli do not accurately predict the outcome. The associability of X is therefore maintained at a relatively higher level in this group than in the true discrimination group, allowing relatively more associative strength to accrue to X over the course of training.

The Pearce-Hall (1980) model is unable to account for related findings such as those reported by Murphy et al. (2001). Like Rescorla and Wagner (1972), Pearce and Hall predict that the presence of C in the true discrimination AX- BX- 2CX+, will reduce the associative strength gained by X to a greater extent than either A or B in the discrimination AX+ BX+ 2CX-, as C in the former discrimination is paired with the outcome on twice as many occasions as either A or B in the latter. Whereas the Pearce-Hall model predicts that more responding to X should be seen in a group that

receives the latter discrimination, Murphy et al. observed that conditioned responding to X was equivalent in the two groups.

The Pearce-Hall (1980) model also fails to account for the IDS/EDS effect. Consider an IDS group that receives the discrimination AW+ BW-, for which the colours A and B are accurate predictors of the outcome, and an EDS group that receives the discrimination AW+ AX-, for which the orientations W and X are accurate predictors of the outcome. Provided the discriminations are solved, the associability of all stimuli in both discriminations will be similarly low, and the loss in attention to the accurate predictors will also be suffered by the stimuli that accompany them. Hence, a subsequent discrimination for which colour is again relevant (CY+ DY-) will be acquired at a comparable rate in both groups, regardless of whether it constitutes an intradimensional or an extradimensional shift.

Although Pearce and Hall (1980) are unable to provide a complete explanation for the findings that have been discussed thus far, the model exclusively predicts Hall and Pearce's (1979) demonstration of negative transfer in conditioning with a single CS. That is, pretraining that involved pairing a CS with a weak US hindered learning about that CS when it was subsequently paired with a stronger US (see also Savastano, Yin, Barnet & Miller, 1998; Hall and Pearce, 1982). Such a finding is inconsistent with Mackintosh's (1975a) principles, which would predict that the initial training with the CS increases its associability, thereby facilitating subsequent learning about that stimulus. The Pearce-Hall model accounts for the negative transfer effect in the following way. As a CS, A, gains increasing associative strength through its pairing with the weak tone, its associability will decline as the discrepancy $|\lambda^{n-1} - V_A^{n-1}|$ gets smaller. On the first trial of conditioning with the stronger shock, λ^{n-1} will be equal to the intensity of the weak shock. As A accurately predicts this outcome, it will not be attended to, and there will be no increase in the associative strength of A.

Only after this trial, when the value of λ^{n-1} represents the strong shock, will there be a discrepancy between the intensity of the shock and the associative strength of A. Such a discrepancy will restore the associability of A, allowing it to gain further associative strength. However, this discrepancy will still be smaller than if pretraining had not been given. Thus increments in the associative strength of A will progress more slowly if it is pretrained than if this initial training had been omitted.

The model can also readily account for a number of findings that cannot be reconciled with the other theories discussed. The design of an experiment by Holland and Gallagher (1993b) is presented in Table 1.6. Two groups of rats received training with a serial compound which comprised a 10-sec presentation of a light (A) which was followed immediately by a 10-sec presentation of a tone (X). This compound was followed by the delivery of food 50% of the time. Group consistent continued to receive this training during a second stage. For group shift, presentations of the AX compound were again reinforced 50% of the time, but were intermixed with presentations of A alone. On a subsequent test, during which A was conditioned with the US, the shift group learnt about A more readily than the consistent group. However, if the subjects had lesions to the central nucleus of the amygdala, the consistent group learnt more readily than the shift group. Although A is an inconsistent predictor of reinforcement during Stage 1, it is an accurate predictor of X in both groups. During Stage 2, in the consistent group it continues to be an accurate predictor of X, but in the shift group it is presented without X. According to the Pearce-Hall model (1980), this arrangement should restore the associability of A in the shift group, enabling associative strength to accrue to this stimulus more rapidly during the test phase than in the consistent group, when the associability of A will be low. It appears that Stage 2 training failed to enhance the associability of A in the shift

group when the subjects had lesions to the central nucleus of the amygdala, that is, damage to the amygdala interfered with the processing of A (see also Holland, 1985).

Table 1.6. Design of the Experiment by Holland and Gallagher (1993b)

Group	Stage 1	Stage 2		Test
Consistent	$A \rightarrow X+/-$	$A \rightarrow X+/-$		A+
Shift	$A \rightarrow X+/-$	$A \rightarrow X+/-$	A-	A+

The Pearce-Hall model (1980) alone also explains the findings of Swan and Pearce (1988). In one of their experiments, four groups of rats received separate reinforced presentations of the stimuli A, B and C. In groups Same-E and Same-I, A and B had the same temporal properties, with each being presented for 10 seconds on half of its presentations, and 30 seconds on the other half. In groups Diff-E and Diff-I, A and B had different temporal properties, one consistently being presented for 10 sec, and the other for 30 sec. In all four groups C was always presented for 10 sec. A serial conditioning stage was then administered, during which the temporal properties of each stimulus remained the same as during initial training, but each presentation of A and B was preceded by a 10-second presentation of stimulus X. Groups Same-E and Diff-E then received excitatory training with X alone, whilst groups Diff-I and Same-I received conditioned inhibition training consisting of reinforced presentations of C, and nonreinforced presentations of CX. During this stage, Swan and Pearce observed greater magazine activity in the presence of X in group Diff-E than in group Same-E. In addition, more magazine activity was evident in the presence of the reinforced stimulus C than the nonreinforced compound CX in group Diff-I, but there was no difference between responding to these two trial types in group Same-I.

Thus learning about X in a novel task was facilitated if it had been followed by stimuli that had different, rather than the same, temporal relations with food. The Pearce-Hall (1980) model can explain this finding in the following way. X could be considered to be an accurate predictor of its consequences in groups Same-E and Same-I as it was consistently followed by stimuli with the same temporal properties, and thus over the course of serial conditioning attention to X would decline. In contrast, X was an inaccurate predictor of its consequences in groups Diff-E and Diff-I as it was followed by stimuli with different temporal properties, and hence attention to this stimulus should be maintained. The greater associability of X in groups Diff-E and Diff-I relative to that in groups Same-E and Same-I would then facilitate subsequent learning about this stimulus.

The Comparator Hypothesis

Despite the successes of the theories described thus far, none has been able to account for all of the results discussed. The common assumption made by these theories is that blocking and relative validity arise from a failure to learn about irrelevant stimuli, and it could be that making this assumption prevents a complete account of the effects that have been observed. Intrinsic to the comparator hypothesis (e.g. Miller and Matzel, 1988) is the assumption that there is no competition between cues for a limited resource such as associative strength or attention during learning. Instead, when a stimulus, X, and a US are presented conjointly, increments in the association between them ($\Delta V_{X, US}$) are determined simply by the salience of X and the US (S_X and S_{US} respectively), as shown in Equation 1.7.

$$\Delta V_{X, US} = S_X * S_{US} * (1.0 - V_{X, US}) \quad (1.7)$$

Decrements in the association between X and this US, when X is presented without the US, are determined by Equation 1.8, where k_1 is a decremental learning parameter ($0 \leq k_1 \leq 1.0$).

$$\Delta V_{X, US} = -k_1 * S_X * V_{X, US} \quad (1.8)$$

According to the principles of the comparator hypothesis, conditioned responding to stimulus X is determined by a comparison that takes place at test, between the associative strength of X, the target, and the associative strength of the stimulus with the strongest association with X that accompanied X during training (the comparator stimulus). Applied to the blocking paradigm, the comparator stimulus is cue A, which is reinforced prior to being conditioned in compound with X, the target cue. An information flow chart of the comparison process that takes place on a subsequent test of X alone is shown in Figure 1.1 (based on a figure from Savastano, Arcediano, Stout and Miller, 2003).

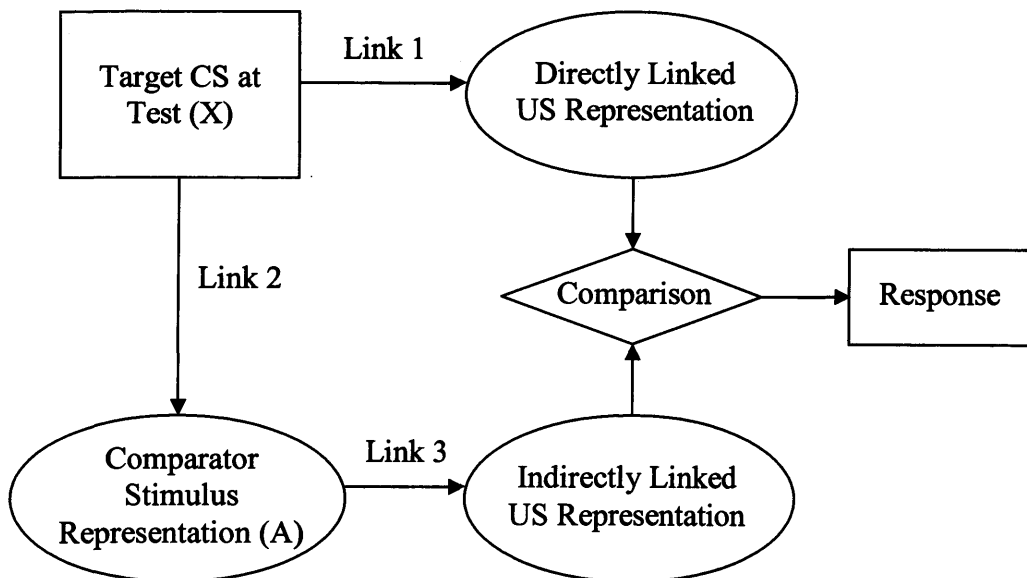


Figure 1.1. The comparator hypothesis.

According to this figure, conditioned responding is a function of Links 1, 2 and 3. Excitatory responding is directly related to the strength of the target-US association (Link 1), and inversely related to the product of the strength of Links 2 and 3. That is, the stronger the target-comparator and comparator-US associations, the weaker the conditioned response (CR). Formally, responding to the target X (R_X) is determined by Equation 1.9.

$$R_X = V_{X, US} - k_2 * f(V_{X, A} * V_{A, US}) \quad (1.9)$$

Thus the comparison that takes place at test is achieved by subtracting $V_{X, A} * V_{A, US}$, the product of the strength of the associations between X and A ($V_{X, A}$, Link 2) and between A and the US ($V_{A, US}$, Link 3) from the strength of the direct association of X with the US ($V_{X, US}$, Link 1). The parameters k and f limit the size of the comparator effect, in line with the observation that cue competition effects are rarely total. When $R_X > 0$, excitatory conditioned responding is observed, when $R_X < 0$, responding indicative of conditioned inhibition is observed.

During the blocking task, pre-training A establishes a strong comparator-US association, thereby strengthening Link 3. The introduction of X in compound with A establishes an X-US association (Link 1), but it also strengthens the A-US association (Link 3) further, and establishes an A-X association (Link 2). Thus, on test, because responding is inversely affected by the strength of the indirectly linked US representation, a small CR is expected to X. In a control group that does not receive pretraining with A, Link 3 is relatively weaker, meaning that the indirectly activated US representation has less influence on responding to X in this group. Consequently a relatively larger CR should be evident on test in the control group than in the blocking group.

Denniston, Savastano and Miller (2001) developed an extended version of the comparator hypothesis, in which all stimuli with an association to the target (with the exception of the US) become comparator stimuli. The stimulus with the strongest association to the target becomes the first-order comparator stimulus, but the effect of this comparator stimulus might be modified by its own comparator stimuli. Correspondingly, Link 2 in Figure 1.1 represents the association between the target and its first-order comparator stimulus, an association which is modulated by any other stimulus that has an association with the target and the first-order comparator, known as a second-order comparator stimulus. Similarly, Link 3 represents the association between the first-order comparator stimulus and the US, which is modulated by any stimuli associated with the first-order comparator stimulus that have also entered into an association with the US. Modulation by second-order comparator stimuli is achieved by applying the comparator process to Links 2 and 3 in Figure 1.1 as well as to Link 1.

As an example, the basic blocking design might be considered as involving reinforced presentations of AC, where C represents the experimental context, followed by conditioning with ACX+. If it is assumed that A is the first-order comparator stimulus for X, then the context is the second-order comparator stimulus for X. A schematic diagram of the comparator processes involved in this conceptualisation of blocking is shown in Figure 1.2, which is based on a diagram from Denniston et al. (2001). From this figure, the associations between X and the context (Link 2.2) and between the context and A (Link 2.3) are able to influence the strength of the X-A association, such that if these links were particularly strong, Link 2 would be weakened. In a similar way, the associations between A and the context (Link 3.2) and between the context and the US (Link 3.3) are able to influence the strength of the association between A and the indirectly linked US representation.

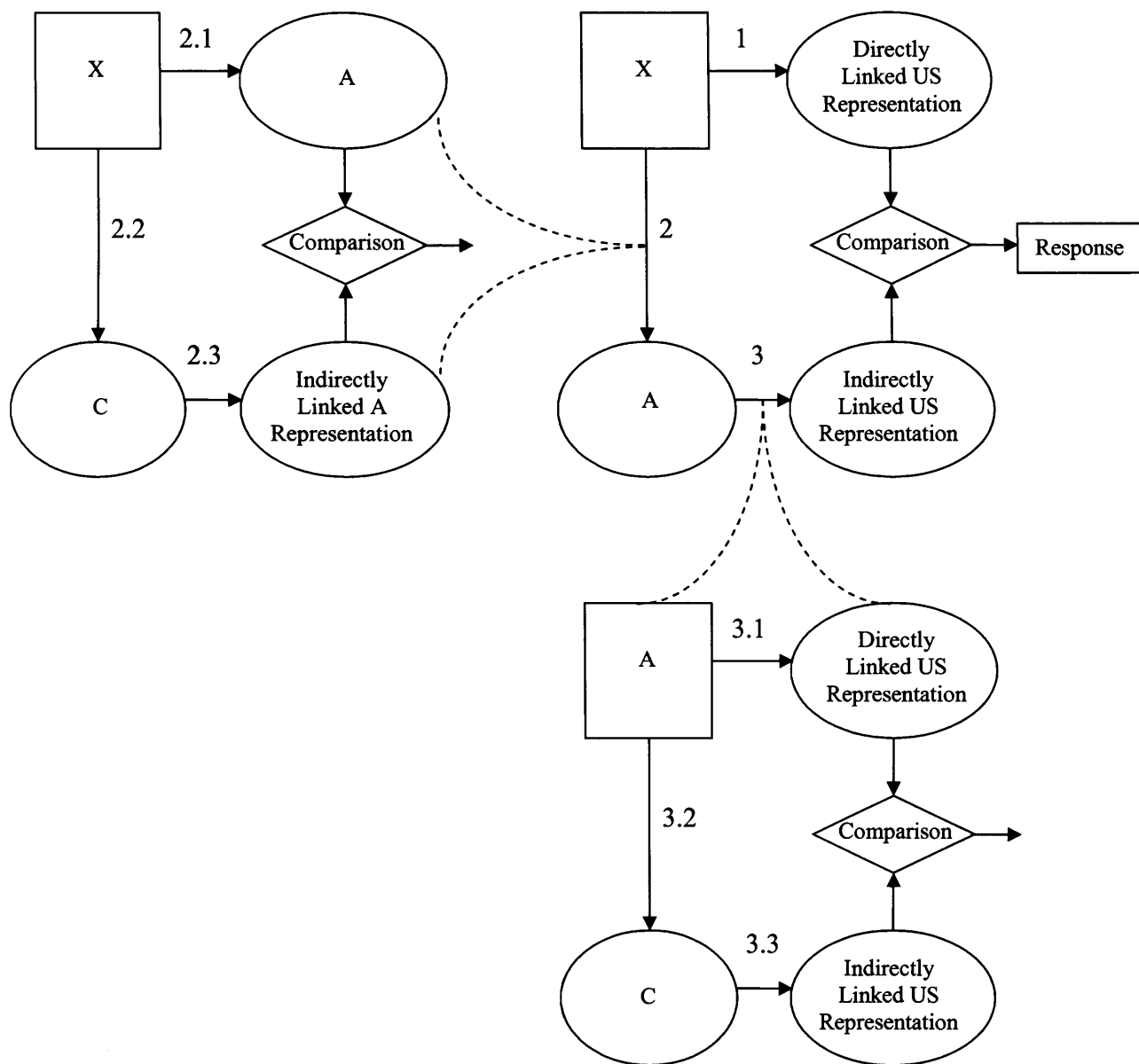


Figure 1.2. The Extended Comparator Hypothesis

One of the successes of the comparator hypothesis and its extended version is the ability to explain Blaisdell et al.'s (1999) finding that responding to X following blocking increased without further training of X. According to the comparator hypothesis, an association between X and the US is formed during the blocking treatment, but A, being the best predictor of the US, interferes with the expression of

this association at test. Thus, if the A-US association is subsequently devalued in some way, X can gain greater behavioural control without being presented itself.

Blaisdell et al.'s (1999) result has important implications for the theories of learning discussed thus far, but the effect has proved difficult to replicate. Holland (1999), for example, failed to find evidence of recovery from blocking when similar training to that given by Blaisdell et al. was administered, but with an appetitive US. There was no evidence that conditioned responding to X was enhanced following extinction trials with A relative to when no extinction trials had been administered. Comparable findings were reported in an experiment by Rauhut, McPhee, DiPietro and Ayres (2000), which involved aversive conditioning with A and AX followed by training designed to convert A into a conditioned inhibitor. Despite this attempt to counter the excitatory A-US association, there was no evidence that the treatment affected responding on a subsequent test of X alone. Indeed, Blaisdell et al. only observed recovery from blocking after administering 'massive extinction' of 800 trials, yet it is not clear from either the comparator hypothesis or its extended version why such prolonged extinction might be required for the effect to be observed. The demonstration of this effect represents a significant challenge to other theories of learning, which warrants further investigation into precisely the conditions that give rise to it.

It is less clear how the comparator hypothesis might be applied to other findings related to blocking. Consider the experiment by Dickinson et al. (1976). As a result of being paired with two shocks during pretraining, A might be expected to indirectly activate a particularly strong representation of the US when it acts as the comparator stimulus for X on test. Presumably, this representation will be activated to a greater extent than when each pretraining trial with A is followed by one just shock.

Therefore, rather than observing an attenuation of the blocking effect, an accentuation of blocking is predicted.

The original comparator hypothesis accounts for the relative validity effect in the following way. According to Cole, Barnet and Miller (1995), A will be the comparator stimulus for X. In the true discrimination (AX+ BX-), A is the most effective comparator for X due to the strong X-A association (Link 2), and the strong A-US association (Link 3), established as a result of the AX+ trials. As A is consistently reinforced in this group, the A-US association (Link 3) will be stronger in the true discrimination group than in the pseudo discrimination group, when A is reinforced following just 50% of its presentations. As responding to X is inversely affected by the strength of the A-US association, the prediction is that relatively less responding to X will be evident in the true discrimination group than in the pseudo discrimination group.

This application of the comparator hypothesis is able to account for the results of Murphy et al. (2001). For group TD1, who received the discrimination AX- BX- 2CX+, C is the comparator stimulus for X as it has a strong association with both X and the US. For the same reason either A or B is the comparator stimulus for X in group TD2, who received the discrimination AX+ BX+ 2CX-. Before asymptote, the comparator-US association (Link 3 in Figure 1.1) will be stronger in group TD1 than in group TD2, as C is paired with reinforcement on twice as many trials in group TD1 as A or B in group TD2. Link 2 will also be stronger in group TD1 because X is paired with its comparator in this group, C, on twice as many occasions as X is paired with its comparator, either A or B, in group TD2. The inverse effect of Links 2 and 3 on responding to X would therefore be greater in TD1 than in TD2, and hence less responding to X is predicted in group TD1 than in group TD2, the same prediction as that made by the Rescorla-Wagner model (1972). At asymptote however, the strength

of Links 2 and 3 will be the same in the two groups, and so equal levels of responding to X should be observed in groups TD1 and TD2. In line with this prediction, Murphy et al. (2001) observed comparable levels of responding in the two groups.

The application of the extended version of the comparator hypothesis to relative validity is rather more complex. According to Blaisdell and Miller (2001), in order for this effect and the findings of Murphy et al. (2001) to be predicted, specific parameters must be assumed. Blaisdell and Miller acknowledged that such an account is “surely less pleasing” (p55) than alternative interpretations that are not parameter dependent. For this reason, the original comparator hypothesis seems to provide a better explanation for these findings.

Finally, the comparator hypothesis cannot explain the IDS/EDS effect. The true discriminations involved in IDS training might be AW+ BW-, AX+ BX-, and those on test CY+ DY-, CZ+ DZ-. There is no mechanism within the comparator hypothesis or its extended version that allows it to account for the finding that this group learnt the test discrimination more quickly than a group that received the training discriminations AW+ AX-, BW+ BX-.

Summary

None of the theories that I have evaluated during this chapter provides an adequate explanation for all of the results related to blocking and relative validity that have been reported in the animal learning literature. However, each potentially contributes to a complete understanding of the fate of irrelevant stimuli by individually accounting for results that the others do not anticipate. The Rescorla-Wagner model (1972) successfully accounts for blocking and relative validity, but is unable to account for certain findings related to blocking, and the IDS/EDS effect. It does however account for one-trial blocking, which the theories of Mackintosh

(1975a) and Pearce and Hall (1980) fail to anticipate. Of these two attentional theories, Mackintosh (1975a) alone accounts for the IDS/EDS effect, but the Pearce-Hall (1980) model exclusively predicts the negative transfer that occurs when a CS is paired with a large US after initially being paired with a small US. Finally, the comparator hypothesis fails to account for effects that have been attributed to changes in attention, but is the only theory to predict retrospective revaluation.

Owing to the difficulties that each of these theories encounters, it appears that a hybrid theory, such as that proposed by Le Pelley (2004) is required. Precisely which components of the theories evaluated should be included in such a model is the focus of this thesis. Perhaps the greatest success of the comparator hypothesis is its ability to explain recovery from blocking, but the lack of replication of this effect casts doubt over whether the inclusion of a mechanism that predicts it is critical. There is more convincing evidence that attention plays an important role in learning about relevant and irrelevant stimuli, although further evidence of the involvement of attentional processes is required before their precise role can be determined. In the next four chapters I shall present experiments which address these issues, before discussing the implications of my results for hybrid theories.

2. Evaluation of the Rescorla-Wagner (1972) and Comparator Hypothesis Accounts of Blocking

Introduction

As described in Chapter 1, in a typical blocking experiment pairings of a compound comprising two stimuli, A and X, with an unconditioned stimulus (US) are preceded by pairings of just A with the US (A+ then AX+). Subsequent responding to X is then found to be weaker than if the original training with A is omitted. With the exception of the comparator hypothesis, each of the theories discussed in Chapter 1 assumes that blocking is a consequence of cues competing for a limited resource, whether that is associative strength (Rescorla-Wagner, 1972) or attention (Mackintosh, 1975a; Pearce & Hall, 1980). As the outcome that follows AX trials is already fully predicted by A, X is irrelevant to the outcome, and will gain little of this resource.

The comparator hypothesis (Miller and Schachtman, 1985; see also Miller & Matzel, 1988) on the other hand makes the assumption that the growth of an association between X and the US is unaffected by the properties of A. Instead, blocking is attributed to a comparison that takes place at test, between the associative strength of X and the associative strength of A. There will be a stronger A-US association in a blocking group that receives initial A+ trials than in a control group for which these trials are omitted. According to the comparator hypothesis, this arrangement should result in X eliciting less responding at test in the former group than in the latter.

In this chapter I evaluate these two opposing assumptions, focusing on the predictions of the Rescorla-Wagner (1972) model versus those of the comparator hypothesis for an extended version of the blocking procedure. The aim of the three

experiments reported here is to gain a clearer understanding of the fate of the irrelevant stimulus X during this paradigm.

The Rescorla-Wagner model (1972) assumes that the associative strength of a stimulus can be modified only if it is physically present. Thus presentations of A, either by itself or paired with the US, after blocking should have no impact on responding to X. In contrast, the comparator hypothesis allows that performance to X can be affected by subsequent manipulations of the associative strength of A. Presenting A in extinction following A+ then AX+ training will weaken the A-US association, allowing X to elicit a stronger response on a subsequent test than if the extinction treatment with A had been omitted. The opposite outcome is expected if conditioning rather than extinction trials are given with A after the A+ and AX+ training.

As mentioned in Chapter 1, several experiments have attempted to evaluate these contrasting predictions, with mixed results. Blaisdell, Gunther and Miller (1999) report findings consistent with the claim that training with A following blocking should give rise to what is referred to as a retrospective revaluation effect. In contrast to this result, Miller, Schachtman and Matzel (1988, unpublished study cited in Blaisdell et al.) failed to find any evidence of retrospective revaluation following blocking, with similar failures being reported by Holland (1999) and Rauhut et al. (2000).

A possible explanation for these conflicting results is that the attempt to abolish the excitatory influence of the comparator cue may not have been effective in the studies of Holland (1999) and Rauhut et al. (2000). Holland gave over five hundred extinction trials with this cue to reduce its associative strength before testing the target and Rauhut et al. went one step further by training the comparator cue as a conditioned inhibitor. Nonetheless, it is possible that these treatments did not have the

intended effect on the excitatory properties of the target cue, with the result that retrospective revaluation was not observed. Taking this possibility into consideration, a different method for testing for retrospective revaluation was used in the present experiments. The rationale behind the method can be appreciated by considering the design of Experiment 1, which is shown in Table 2.1.

Table 2.1. Design of Experiment 1.

Group	Stage 1		Stage 2	Test 1	Stage 3		Test 2
Blocking	A+	B-	AX+	X-	A-	B+	X-
Control	A-	B+	AX+	X-	A+	B-	X-

During Stage 1, a blocking group received discrimination training in which A was paired with food and B was not. A control group received the opposite discrimination. Both groups then received conditioning with AX during Stage 2, followed by a test with X alone, which was expected to reveal stronger responding in the control than in the blocking group. A reversal of Stage 1 training was given in Stage 3, in order to reverse the significance of A in both groups. Thus Stage 3 involved an A- B+ discrimination for the blocking group and an A+ B- discrimination for the control group. Finally, both groups received a second test with X by itself.

According to the comparator hypothesis, the training given in Stage 2 will ensure that the associative strength of the blocked stimulus, X, will not differ between the two groups during either Test 1 or Test 2. Performance on these tests will then depend upon the associative strength of A at the time of testing. Due to the discrepant training received by the two groups during Stage 1, A will have more associative strength in the blocking group than in the control group on Test 1. As the strength of the A-US association is assumed to have an inverse effect on responding to X,

responding on Test 1 should be weaker in the blocking group than in the control group. As a result of the Stage 3 training, on Test 2 A will have weak associative strength in the blocking group and high associative strength in the control group. Therefore this training should result in the outcome of Test 2 being opposite to that of Test 1, with weaker responding to X in the control group than in the blocking group. A particular advantage of this design is that it will be possible to compare the associative strengths of A between the two groups during Stage 3. In contrast to the studies by Holland (1999) and Rauhut et al. (2000), it will therefore not be possible to attribute a failure to confirm the prediction from the comparator hypothesis to a failure to manipulate adequately the associative strength of A.

In summary, if a stronger conditioned response to X is observed during the second test in the blocking group than in the control group after the demonstration of a standard blocking result on Test 1, it can be inferred that retrospective revaluation has occurred. Such an outcome would not be compatible with the Rescorla-Wagner theory (1972) which predicts that responding to the target will be weaker in the blocking than the control group during both the first and the second test.

Experiment 1

Method

Subjects. The subjects were 16 experimentally naïve male, hooded Lister rats. They were approximately 6 months old at the start of the experiment. Prior to the experiment they were gradually reduced to 80% of their free-feeding weights and were maintained at this level throughout the experiment by being fed a restricted amount after each experimental session. The rats were housed in pairs in a light-proof room in which the lights were on for 14.5 hours each day. They were tested at the

same time on successive days during the period when the lights were on in their holding room.

Apparatus. Four identical conditioning chambers were used. The side walls and ceiling of each chamber were constructed from clear Perspex. Each wall had a height of 28 cm and a width of 30 cm. There was a grid floor positioned 5 cm above the base of the chamber. In the centre of the back wall, there was a circular hole, diameter 3 cm, the centre of which was 3 cm above the grid floor. The circular hole allowed access to a well into which sucrose solution (8% sugar, 92% water) was delivered. This area is henceforth referred to as the magazine. A peristaltic pump was located beneath each conditioning chamber which delivered the sucrose solution via a plastic tube into the well. The arrangement of this apparatus is shown in Figure 2.1. A PC with Whisker software (Cardinal, 2000) and programmed in Visual Basic 6.0 (Microsoft Corporation, Redmond, WA), controlled the experimental events and recorded the duration of entries into the magazine from infrared sensors that were set into each chamber. Barriers were placed between the chambers to prevent the animals seeing each other.

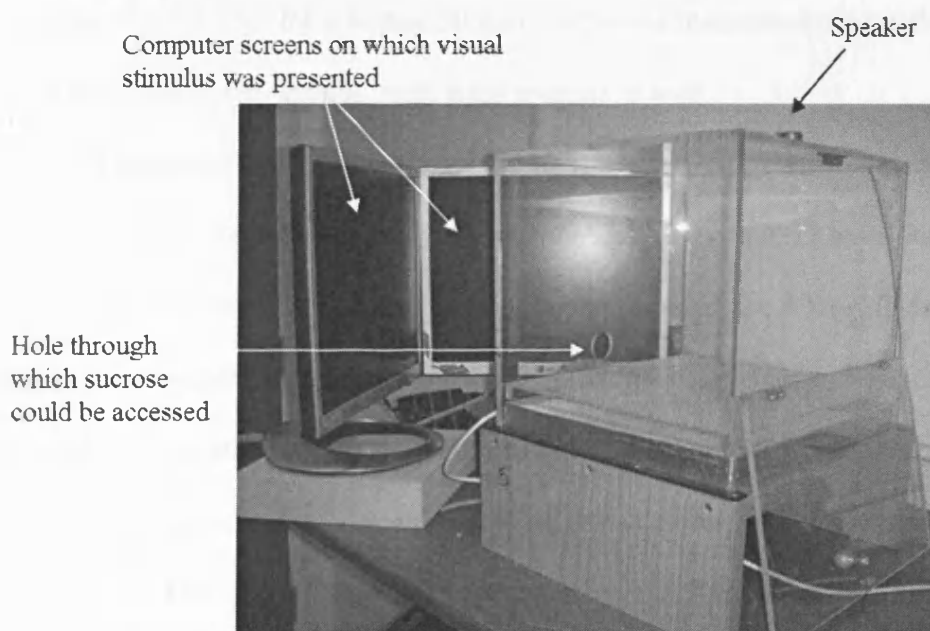


Figure 2.1. Arrangement of the apparatus used in Experiments 1-3.

Auditory stimuli were delivered simultaneously to all chambers from a 5-ohm speaker located on the ceiling of each chamber. Visual stimuli appeared on two flat-screen thin film transistor (TFT) monitors that had a width of 33 cm and a height of 27 cm. These were placed side by side at an angle of 90°, and positioned in front of each chamber. The screens joined at 25 cm in front of each conditioning chamber, in line with the centre of the hole in the back wall. The bottom edge of each screen was level with the floor of the chamber.

The auditory stimuli were a 10-Hz, 70-dB clicker and a 2-kHz, 70-dB tone. The visual stimulus was the illumination of one of the screens to white. For half of the animals, this was the left-hand screen, for the others it was the right-hand screen. The stimuli were counterbalanced, such that for half of the animals within each group A was the clicker and B the tone, and for the other half A was the tone and B the clicker. X was always the white stimulus.

Procedure. All rats initially received two sessions of magazine training. During each of these 1-hr sessions, 0.2ml of sucrose solution was delivered into the well over a period of 3 sec, every 1 min for 30 min. The rat remained in the conditioning chamber for a further 30 min. Following magazine training, the animals were divided into two groups, with eight animals in each.

There were 24 trials in each of the 10 sessions of Stage 1. All animals received 12 trials during which the clicker was presented for 10 sec, and 12 trials during which the tone was presented for 10 sec. Unless otherwise stated, the following details applied to all stages of this experiment and subsequent experiments. The inter-trial interval (ITI) ranged from 80 s to 160 sec, with a mean of 120 sec. For all groups, the sequence of reinforced and nonreinforced trials was random, with the constraint that no more than two trials of the same type could occur in succession. The duration spent in the magazine was recorded during each 10-sec presentation of the stimulus.

Reinforcement constituted a 0.2 ml delivery of sucrose into the well over a period of 3 sec. In the blocking group, presentations of stimulus A were immediately followed by reinforcement. These trials were nonreinforced for the control group. Presentations of stimulus B were reinforced for the control group, and nonreinforced for the blocking group.

The first session of Stage 2 began on the day after the final session of Stage 1. In each of the four sessions of Stage 2, animals received eight trials during which presentations of a compound stimulus were reinforced. For all animals, this compound consisted of the simultaneous presentation of A (the stimulus that had been reinforced in the blocking group in Stage 1, and nonreinforced in the control group), and X, the white stimulus. Although a third of the number of trials was presented, the sessions were the same length as those from Stage 1. For this reason, during the four sessions of this stage the ITI ranged from 230 sec to 390 sec with a mean of 313 sec.

The next session, which was on the day following the final session of Stage 2, served as a test of the white stimulus (X). Both groups first received five reinforced trials with AX, which were followed by three trials during which 10-sec presentations of the white stimulus were nonreinforced. As in Stage 2, the mean ITI during this test session was 313 sec.

On the following day, each group received the first of seven sessions which involved a reversal of the training they had received in Stage 1. Presentations of stimulus B were reinforced in the blocking group, and nonreinforced in the control group. Presentations of A were reinforced in the control group, and nonreinforced in the blocking group. The remaining procedural details were the same as for Stage 1.

Subjects were returned to the apparatus for a final test session on the day after session seven of Stage 3. During this session, each group received 21 trials made up of the trial types they received in Stage 3. Both groups then received 3 trials on which

the white stimulus was presented for 10 sec. As in Stage 3, the ITI ranged from 80 sec to 160 sec, with a mean of 120 sec.

Results

A Type 1 error rate of $p < .05$ was adopted for all of the statistical tests in this experiment and those that follow. The results from the three stages of training are shown in Figure 2.2. For both groups, the mean duration of magazine activity during presentations of each CS for every session of Stage 1 is presented in the left-hand panel of Figure 2.2. By the end of Stage 1, blocking and control animals were spending a comparable amount of time in the magazine during presentations of the reinforced stimulus, and this was considerably longer than the duration spent in the magazine during nonreinforced trials. The mean duration of magazine activity during each trial type on the final two sessions was calculated for every subject. A two-way analysis of variance (ANOVA) of individual mean durations of magazine activity was conducted with the factors of trial type (reinforced and nonreinforced) and group (blocking or control). This analysis revealed a significant effect of trial type, $F(1, 14) = 370.30$, $MSE = 0.34$, but no effect of group and no Trial Type x Group interaction, $F_s < 1$.

The data for the four sessions of Stage 2, in which reinforced trials with AX were given, are presented in the centre panel of Figure 2.2. The mean duration of magazine activity during presentations of AX in the control group was initially less than in the blocking group, presumably due to the fact that A was nonreinforced in the control group in Stage 1, and reinforced in the blocking group. However, by the end of training, both groups responded at the same high level to AX. A t-test based on mean individual durations of responding during the final two sessions of this stage confirmed that there was no significant effect of group, $t(14) = .44$.

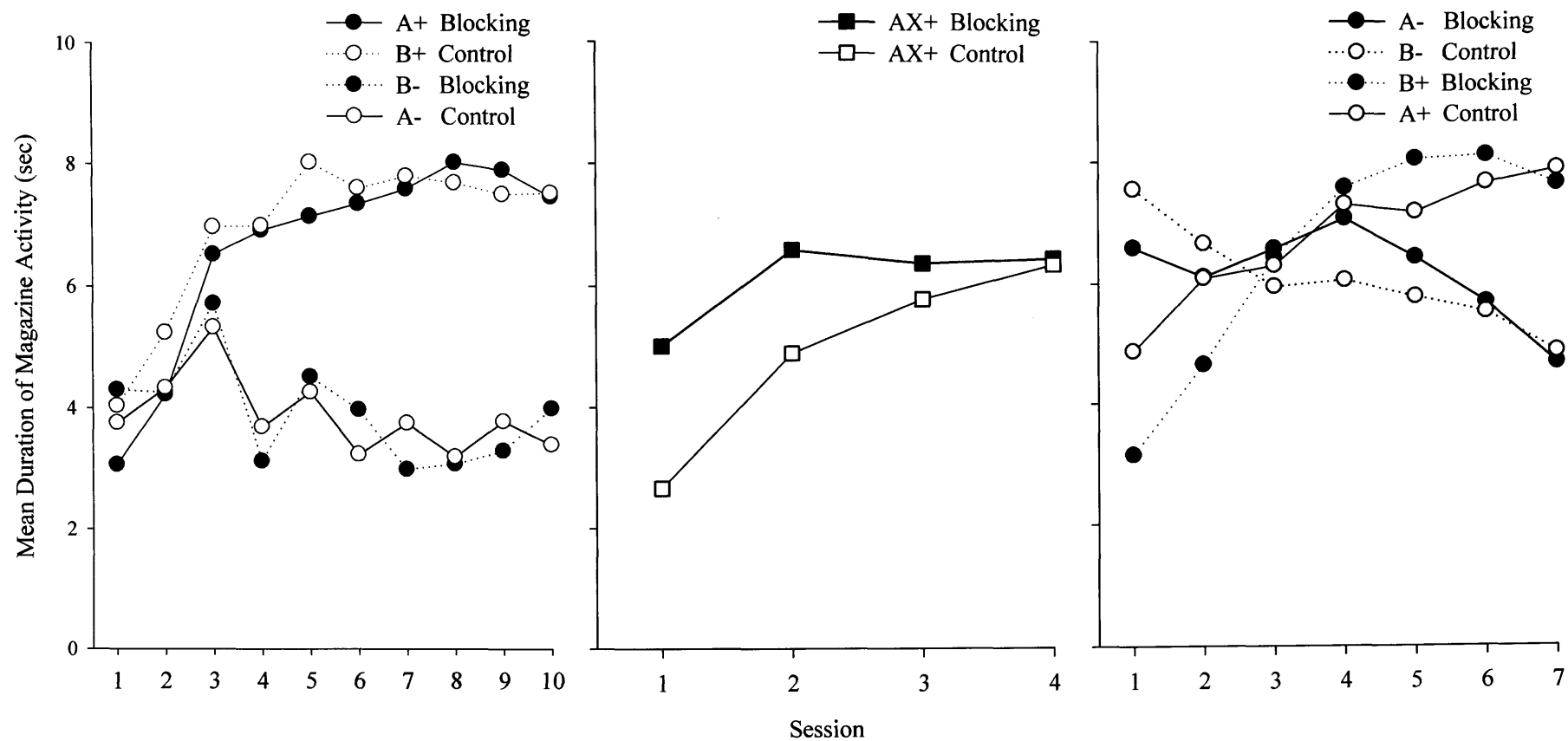


Figure 2.2. Mean duration of magazine activity for both groups during presentations of each trial type on each session of Stage 1 (left-hand panel), Stage 2 (centre panel) and Stage 3 (right-hand panel) of Experiment 1.

The mean durations of magazine activity for both groups during presentations of the stimuli in Stage 3 are presented in the right-hand panel of Figure 2.2. Stage 3 involved a reversal of Stage 1 training. A t-test conducted on the mean individual durations of magazine activity during presentations of A on the final two sessions confirmed that the reversal treatment was effective, such that by the end of this stage the control group spent significantly longer in the magazine during presentations of A than the blocking group, $t(14) = 5.20$. A corresponding analysis revealed that the treatment had also effectively reversed the significance of B in the two groups, with the blocking group spending significantly longer in the magazine during presentations of this stimulus than the control group, $t(14) = 3.57$.

The mean durations of magazine activity during presentations of X for Test 1 and Test 2 were calculated for both groups. These data are presented in Figure 2.3. From this figure it is evident that responding to X was stronger in the control group than the blocking group on both the first and the second test of this stimulus. A two-way ANOVA with the factors of group (blocking or control) and test (1 and 2) confirmed this observation, revealing a significant effect of group, $F(1, 14) = 6.16$, $MSE = 5.17$, and a non-significant Test x Group interaction, $F(1, 14) = 1.25$, $MSE = 2.32$. Thus the blocking of X caused by conditioning in Stages 1 and 2 was not affected by the reversal training with A in Stage 3. The ANOVA also revealed a significant effect of test, $F(1, 14) = 8.02$, $MSE = 2.32$, reflecting the decrement in responding observed on Test 2 relative to that seen on Test 1. This effect can be explained either by the extinction trials with X received during Test 1, or simply by the passage of time between the two tests.

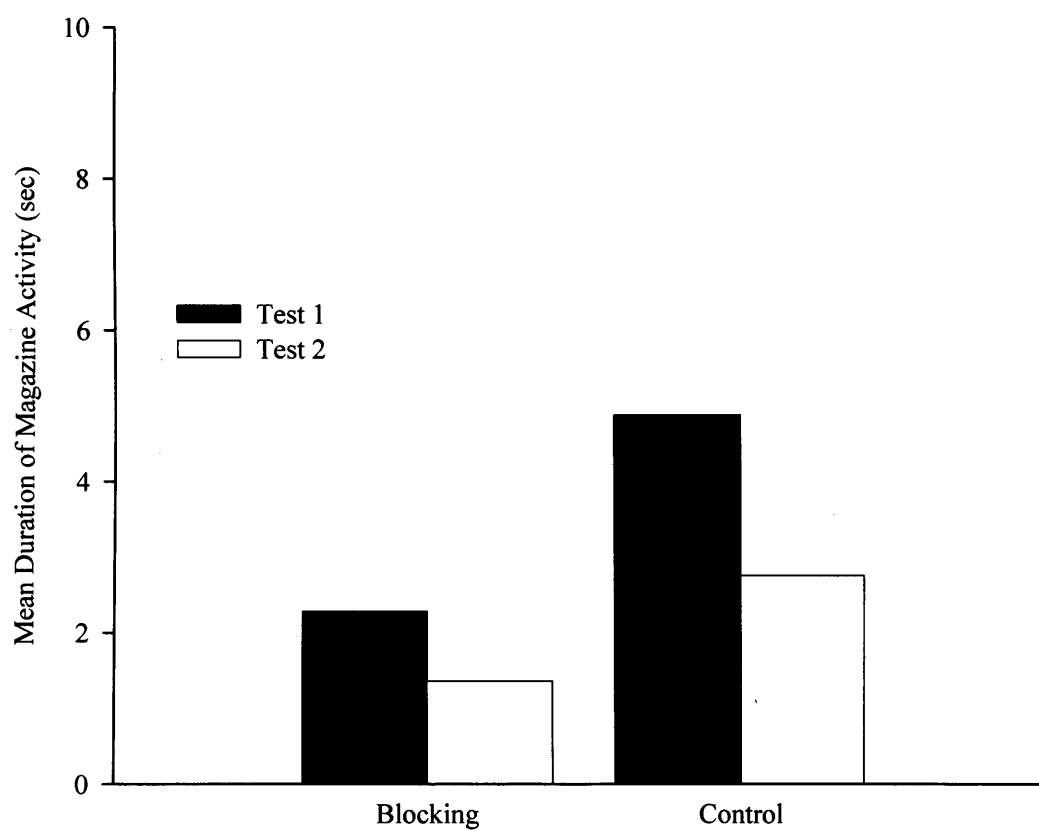


Figure 2.3. Mean duration of magazine activity for both groups during presentations of X on Tests 1 and 2 of Experiment 1.

Discussion

The results of the first test of X in Experiment 1 support standard associative models of learning (e.g. Rescorla and Wagner, 1972) and the comparator hypothesis in that reinforced trials with A, followed by conditioning with the compound AX resulted in responding to X that was diminished relative to that observed in a control group. However, the comparator hypothesis is unable to explain the finding that following revaluation of A, this pattern of responding remained. Standard associative models on the other hand predict this finding. Experiment 2 was conducted to test the generality of this effect with a different blocking design.

Experiment 2

The design of Experiment 2 was based on Experiment 1 with two key differences. First, for both groups, presentations of the compound in Stage 2 were intermixed with the training trials received in Stage 1 (see Table 2.2). This training was given to maximise the associative strength gained by A in the blocking group and minimise that gained by A in the control group, with the aim of strengthening any blocking effect. Secondly, just two trials with X were given during the first test in an attempt to reduce the effect of these extinction trials with X on the second test of this stimulus. In keeping with the results of Experiment 1, a blocking effect with X was expected on both Test 1 and Test 2.

Table 2.2. Design of Experiment 2.

Group	Stage 1		Stage 2			Test 1	Stage 3		Test 2
Blocking	A+	B-	A+	B-	AX+	X-	A-	B+	X-
Control	A-	B+	A-	B+	AX+	X-	A+	B-	X-

Method

Subjects. The subjects were 16 male, naïve hooded Lister rats. They were approximately 6 months old at the start of the experiment. They were fed and maintained in the same manner as subjects in Experiment 1.

Apparatus. The same apparatus was used in Experiment 2 as in Experiment 1. In addition a further four conditioning chambers of the same design were used, each of which was arranged in relation to two flat-screen TFT monitors in the same way as in Experiment 1. The same stimuli as in Experiment 1 were used, and these were counterbalanced in the same way.

Procedure. Magazine training and the ten sessions of Stage 1 were conducted in the same manner as for Experiment 1 for both the blocking and control groups. The first session of Stage 2 began on the day after the final session of Stage 1. There were 24 trials in each of the 15 sessions of Stage 2. Both groups received eight of each of the trial types presented in Stage 1, in addition to reinforced presentations of the AX compound on the remaining eight trials. The sequence of trials was random, with the constraint that no more than two trials of the same type could occur in succession.

The next session, which was on the day following the final session of Stage 2, served as a test of the white stimulus (X). All animals received 22 trials made up of the trial types they received in Stage 2. The final two trials in the session were 10-sec nonreinforced presentations of the white stimulus.

Stage 3 proceeded in the same manner as in Experiment 1, with all animals receiving seven sessions which involved a reversal of the training they had received in Stage 1. On the day after session 7 of Stage 3, subjects were returned to the apparatus for a final test session which was identical to that given in Experiment 1. For all stages of the experiment the mean ITI was 120 sec (range 80–160 sec). The remaining procedural details were the same as for Experiment 1.

Results

The results from the three stages of training are shown in Figure 2.4. For both groups, the mean duration spent in the magazine during presentations of each CS for every session of Stage 1 is presented in the left-hand panel. By the end of Stage 1, blocking and control animals were spending a comparable amount of time in the magazine during presentations of the reinforced stimulus, and this was considerably longer than the duration spent in the magazine during nonreinforced trials. The mean duration of magazine activity during each trial type on the final two sessions was calculated for every subject. A two-way ANOVA of individual mean durations of responding was conducted, with the factors of trial type (reinforced and nonreinforced) and group (blocking or control). This revealed a significant effect of trial type, $F(1, 14) = 74.92$, $MSE = 1.88$, but no effect of group, $F(1, 14) = 2.63$, $MSE = 1.00$, and no Trial Type x Group interaction ($F < 1$).

The mean durations of magazine activity during the three trial types of Stage 2 are presented in the centre panel of Figure 2.4. During the final two sessions of this stage both groups were spending considerably longer in the magazine during reinforced trials than during nonreinforced trials. A two-way ANOVA with the factors of trial type (reinforced element, nonreinforced element and reinforced compound) and group (blocking or control) revealed a significant effect of trial type, $F(2, 28) = 80.17$, $MSE = 1.19$, but no effect of group, $F(1, 14) = 2.58$, $MSE = 2.18$, and no Trial Type x Group interaction, $F < 1$. Bonferroni corrected pairwise comparisons revealed that responding to the reinforced element was significantly higher than responding to the nonreinforced element, $t(15) = 15.25$, as was responding to the reinforced compound, $t(15) = 7.34$. There was also a significant difference between responding to the reinforced compound and reinforced element, $t(15) = 3.70$.

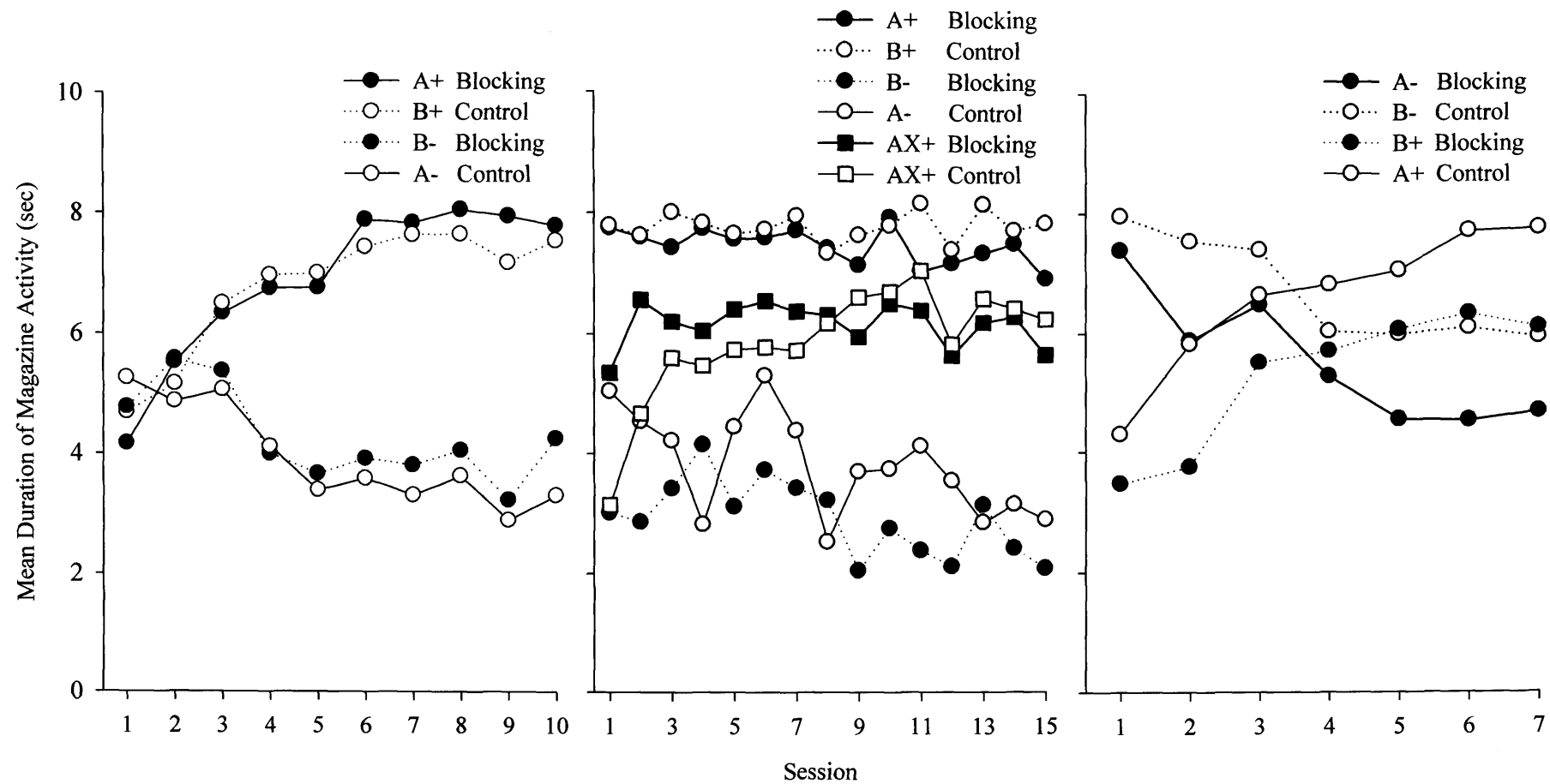


Figure 2.4. Mean duration of magazine activity for both groups during presentations of each trial type on each session of Stage 1 (left-hand panel), Stage 2 (centre panel) and Stage 3 (right-hand panel) of Experiment 2.

This difference in responding to the two reinforced stimuli shown by both groups was presumably due to the compound being a combination of a visual and an auditory stimulus. It is widely acknowledged that orienting responses are displayed toward visual stimuli (e.g. Kaye and Pearce, 1984), which might result in the animal spending less time in the magazine during their presentation.

The mean durations of magazine activity for both groups during presentations of the stimuli in Stage 3 are presented in the right-hand panel of Figure 2.4. From this figure it appears that the training was effective in reversing the significance of A in the two groups. A t-test conducted on the mean individual durations of magazine activity during presentations of A confirmed that during the final two sessions, the control group spent significantly longer in the magazine during presentations of A than the blocking group, $t(14) = 4.35$. Inspection of the right-hand panel of Figure 2.4 indicates that the reversal treatment was not effective for stimulus B. This observation was confirmed by a t-test conducted on the mean individual durations of magazine activity during presentations of B during the final two sessions, $t(14) = .19$. This finding could be explained by the larger difference between the groups in responding to B than in responding to A at the beginning of Stage 3. It could be that the seven sessions of Stage 3 were not sufficient for the reversal of B to occur. Whatever the reason for this result, it must be noted that the critical comparison in this stage is between responding to A in the two groups, as A is the comparator for X, and the reversal treatment was effective for this stimulus.

The mean durations of magazine activity for both groups during presentations of X on Tests 1 and 2 are presented in Figure 2.5. In keeping with the results of Experiment 1, the control group responded more strongly in the presence of X than

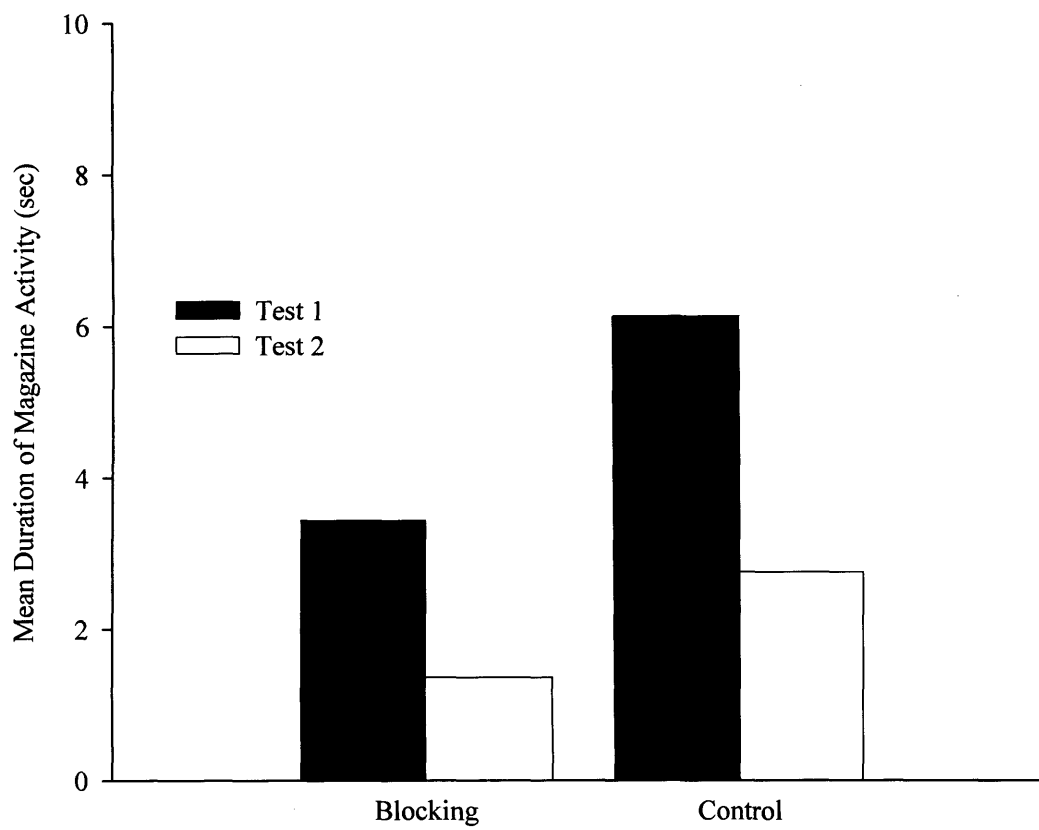


Figure 2.5. Mean duration of magazine activity for both groups during presentations of X on Tests 1 and 2 of Experiment 2.

the blocking group on both tests. Responding on Test 2 was also similarly reduced relative to responding on Test 1. These observations were confirmed by a two-way ANOVA with the factors of group (blocking or control) and test (1 or 2), which revealed a significant effect of group, $F(1, 14) = 7.62$, $MSE = 5.39$, and test $F(1, 14) = 21.90$, $MSE = 1.63$, but no Test x Group interaction, $F < 1$.

Discussion

The results replicated those of Experiment 1, showing that blocking was unaffected by subsequent training in which the competing cue was nonreinforced in the blocking group and reinforced in the control group. The results of Experiment 2 therefore provide further support in favour of standard associative accounts of blocking (e.g. Rescorla and Wagner, 1972).

In Stage 3, both groups received a reversal of the training given in Stage 1. Unexpectedly, this treatment successfully reversed the significance of A in the two groups, but did not have this effect on the significance of B. It is difficult to provide a suitable explanation for this finding, and it should be noted that a reversal in responding to B in the two groups is not required for the predictions of the comparator hypothesis to be realised. The fact the reversal was not observed in Experiment 2 suggests that the training schedule used in Stage 2 of this experiment may have been accountable. However, this effect was not replicated when the same training procedure for Stage 2 was used in Experiment 3.

Experiment 3

In other experiments that have looked for retrospective revaluation only one test of X has been administered, following the stage in which extinction trials with the comparator cue were presented (e.g. Holland, 1999; Blaisdell, Gunther and Miller,

1999). In Experiments 1 and 2, an additional test of X was administered prior to this stage in order to confirm the effectiveness of the Stage-2 blocking treatment. It is conceivable that this initial test might somehow influence responding to X on Test 2, and by doing so prevent observation of the reversed blocking effect that is predicted by the comparator hypothesis. For example, pairing X with a low level of responding in the blocking group, and a (relatively) high level of responding in the control group may have established S-R associations between the test stimuli and these levels of responding that persisted until the second test session. For this reason, Experiment 3 was conducted. Two groups received the same design as that used in Experiment 2. Another two groups received the same training, but Test 1 was omitted (See Table 2.3).

Table 2.3. Design of Experiment 3.

Group	Stage 1		Stage 2			Test 1	Stage 3		Test 2
Blocking-1	A+	B-	A+	B-	AX+		A-	B+	X-
Control-1	A-	B+	A-	B+	AX+		A+	B-	X-
Blocking-2	A+	B-	A+	B-	AX+	X-	A-	B+	X-
Control-2	A-	B+	A-	B+	AX+	X-	A+	B-	X-

Method

Subjects. The subjects were 64 male, naïve hooded Lister rats. They were approximately 6 months old at the start of the experiment. They were fed and maintained in the same manner as subjects in Experiments 1 and 2.

Apparatus. The same apparatus was used in Experiment 3 as in Experiment 2. The auditory stimuli were the same 10-Hz, 70-dB clicker that was used in the previous experiments, and a 500-Hz, 70-dB tone that was repeated at a rate of 2.5 times per second 10 times during a 10-sec trial. Again, the visual stimulus was the

illumination of one of the screens to white. The position of this stimulus and the manner in which the stimuli were counterbalanced was the same as in Experiments 1 and 2.

Procedure. Magazine training was conducted in the same way as in Experiments 1 and 2. In Stage 1 and Stage 2 training, both blocking and both control groups received the same training as the blocking and control group respectively in Experiment 1.

On the day following the final session of Stage 2 all four groups received 21 training trials from this stage. Groups blocking-2 and control-2 then received an additional three test trials with the white stimulus, as in Test 1 from Experiment 1. Groups blocking-1 and control-1 did not receive any test trials following the training trials, but remained in the apparatus for the same amount of time as the other two groups.

As in the previous experiments, on the following day, each group received the first of seven sessions which involved a reversal of the training they had received in Stage 1. All four groups then received a test session which was conducted in the same manner as Test 2 in Experiments 1 and 2. Procedural details that have been omitted were the same as for Experiment 1.

Results

The results from the three stages of training are shown in Figure 2.6 for the blocking-1 and control-1 groups and in Figure 2.7 for the blocking-2 and control-2 groups. For all four groups, the mean duration spent in the magazine during presentations of each CS for every session of Stage 1 is presented in the left-hand panels of Figures 2.6 and 2.7. By the end of Stage 1, both blocking and both control groups were spending a comparable amount of time in the magazine during

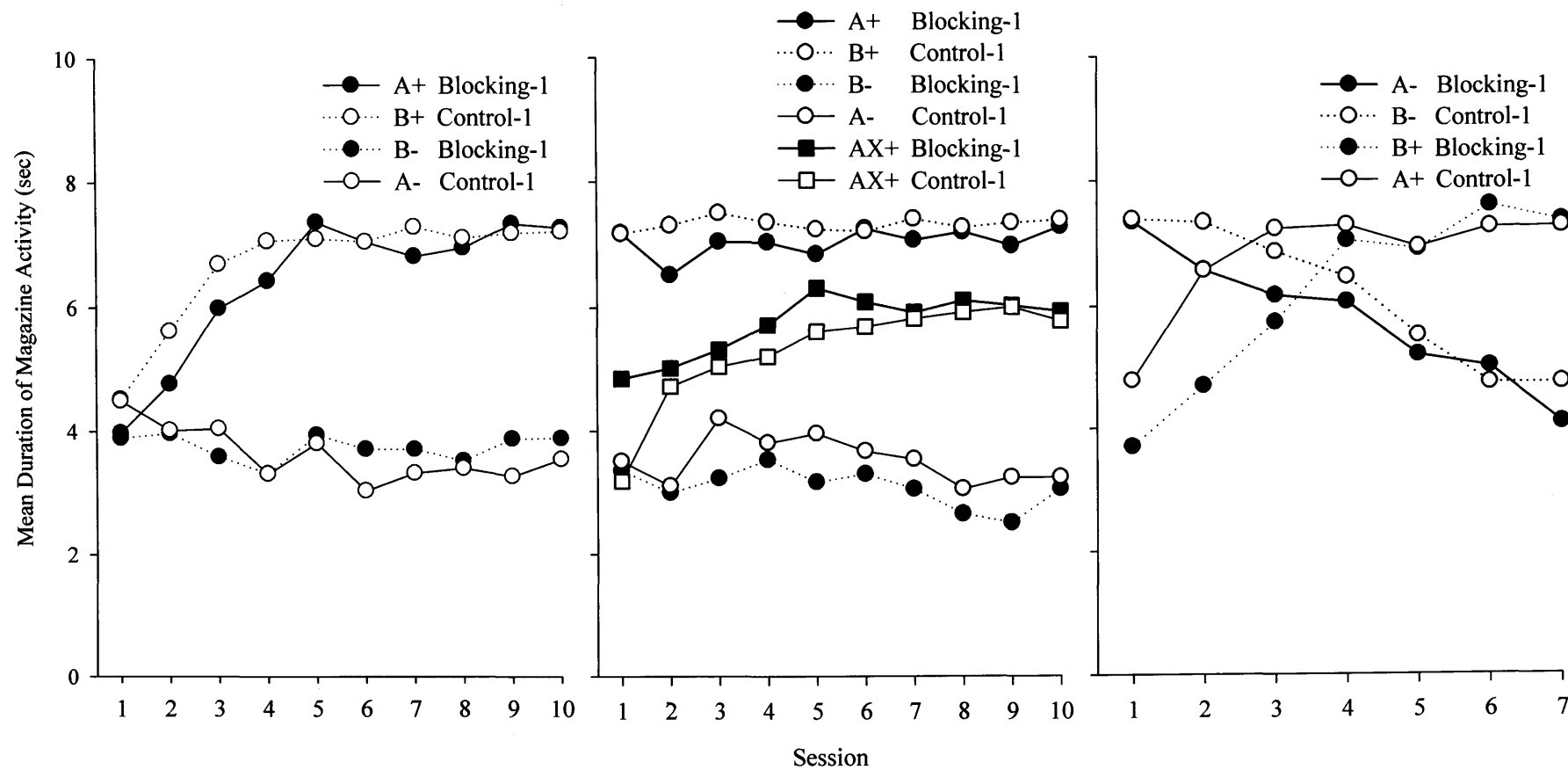


Figure 2.6. Mean duration of magazine activity for groups blocking-1 and control-1 during presentations of each trial type on each session of Stage 1 (left-hand panel), Stage 2 (centre panel) and Stage 3 (right-hand panel) of Experiment 3.

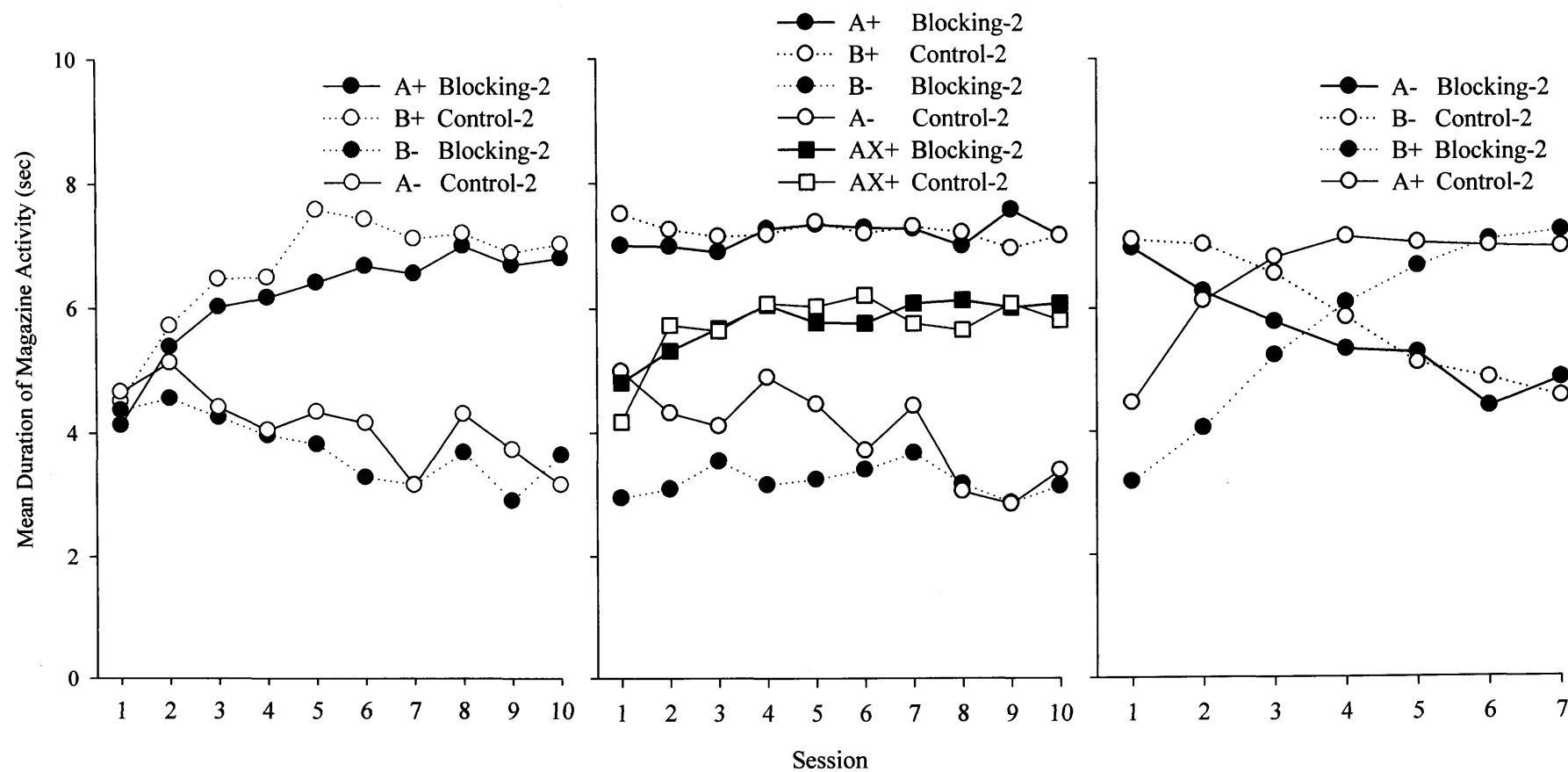


Figure 2.7. Mean duration of magazine activity for groups blocking-2 and control-2 during presentations of each trial type on each session of Stage 1 (left-hand panel), Stage 2 (centre panel) and Stage 3 (right-hand panel) of Experiment 3.

presentations of the reinforced stimulus, and this was substantially longer than the duration spent in the magazine during presentations of the nonreinforced stimulus.

The mean duration of magazine activity during each trial type on the final two sessions of Stage 1 was calculated for every subject. A three-way ANOVA of individual mean durations of magazine activity was conducted with the factors of trial type (reinforced and nonreinforced), group (blocking or control) and number of tests (1 or 2). The analysis revealed a significant effect of trial type, $F(1, 60) = 206.34$, $MSE = 1.96$, but no effect of group, $F < 1$, or number of tests, $F(1, 60) = 1.11$, $MSE = 3.40$. None of the interactions was significant ($F_s < 1$).

The data for the three trial types of Stage 2 are presented in the centre panels of Figures 2.6 and 2.7. By the end of training, both blocking and control groups were spending considerably longer in the magazine during presentations of both reinforced trial types than during presentations of the nonreinforced stimulus, although the duration of responding to the compound stimulus was slightly less than to the stimulus reinforced during Stage 1. A three-way ANOVA of mean individual durations of magazine activity during the final two sessions of Stage 2 was conducted, with the factors of trial type (reinforced element, nonreinforced element and reinforced compound), group (blocking or control) and number of tests (1 or 2). This revealed a significant effect of trial type, $F(2, 120) = 251.05$, $MSE = 1.20$, but there was no effect of group or number of tests and none of the interactions was significant, $F_s < 1$. Subsequent Bonferroni corrected pairwise comparisons revealed that there was a significant difference between the durations of responding to the reinforced element and nonreinforced element, $t(63) = 18.84$, and between the durations of responding to the reinforced compound and nonreinforced element, $t(63) = 14.85$. As in Experiment 2, there was also a significant difference between responding to the reinforced compound and reinforced element, $t(63) = 9.30$.

The mean durations of magazine activity for the groups during presentations of the stimuli in Stage 3 are presented in the right-hand panels of Figures 2.6 and 2.7. From these panels it appears that this training was effective in reversing the significance of both A and B in all groups. A two-way ANOVA conducted on the mean individual durations of magazine activity during presentations of A on the final two sessions, with the factors of group (blocking or control) and number of tests (1 or 2), revealed a significant effect of group, $F(1, 60) = 44.77$, $MSE = 2.34$, but no effect of number of tests, or Group x Number of tests interaction, $F_s < 1$. This analysis therefore confirmed that both control groups spent significantly longer in the magazine during presentations of A than the blocking groups, and that the durations of responding to this stimulus were comparable whether subjects received two tests with X or just one.

The same analysis was conducted on responding during B on the final two sessions. This analysis also revealed a significant effect of group, $F(1, 60) = 51.66$, $MSE = 2.13$, but no effect of number of tests, or Group x Number of tests interaction, $F_s < 1$. Thus both blocking groups spent significantly longer in the magazine during presentations of B than the control groups. Taken together, the results from both ANOVAs confirmed that in all groups Stage 3 training successfully reversed the significance of both stimuli involved in Stage 1.

During Test 1, the blocking-2 and control-2 groups received three test trials with X. The mean duration of magazine activity during these trials is shown in the left-hand panel of Figure 2.8. From this figure it is evident that during presentations of X, group control-2 spent longer in the magazine than group blocking-2. A t-test conducted on the mean individual durations of magazine activity during presentations of X revealed a significant effect of group, $t(30) = 2.37$.

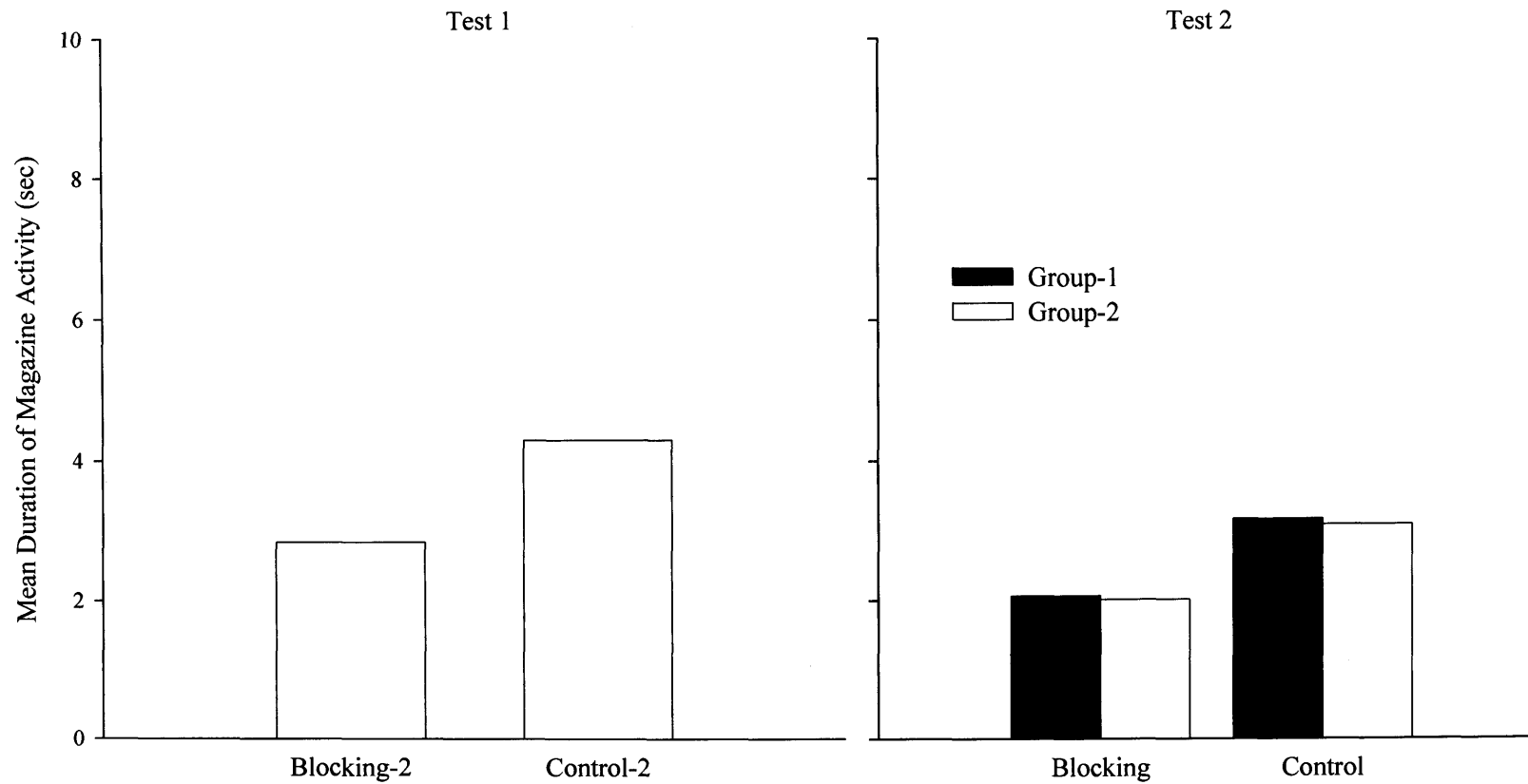


Figure 2.8. Mean duration of magazine activity for groups blocking-2 and control-2 during presentations of X on Test 1 (left-hand panel), and for all four groups during presentations of X on Test 2 (right-hand panel) of Experiment 3 (Group-1 refers to groups blocking-1 and control-1; Group-2 refers to groups blocking-2 and control-2).

The mean durations of magazine activity for all four groups during presentations of X on Test 2 are presented in the right-hand panel of Figure 2.8. From this figure it is evident that groups control-1 and control-2 spent comparable durations in the magazine, which were considerably longer than the similar durations that groups blocking-1 and blocking-2 spent in the magazine. Accordingly, a two-way ANOVA with the factors of group (blocking or control) and number of tests (1 or 2) revealed a significant effect of group, $F(1, 60) = 9.32$, $MSE = 2.01$, but no significant effect of number of tests and no Group x Number of tests interaction, $F_s < 1$.

Discussion

The results of Experiment 3 replicate those of Experiments 1 and 2, suggesting that the failure for revaluation of the competing cue to influence blocking in this paradigm is a robust effect. The lack of a difference between the control groups and between the blocking groups during Test 2 indicates that an initial test of X prior to revaluation with the competing cue does not influence subsequent responding to X.

In all three experiments, a reduction in responding in both the blocking and control groups from Test 1 to Test 2 was observed. In Experiment 3, a comparably low level of responding during Test 2 was observed in groups that received either one or two tests with X, which suggests that the reduction in responding to X observed on Test 2 was due to the passage of time, rather than to the extinction trials with X in Test 1.

General Discussion

In three experiments a blocking group of rats received reinforcement with A which either preceded conditioning with AX, or preceded and accompanied conditioning with AX. Subsequent testing with X in each experiment revealed weaker responding than in a control group that received similar treatment, but A by itself was not reinforced. The more important finding from the experiments is that these demonstrations of blocking were unaffected by subsequent training in which A was paired with food in the control group but presented without food in the blocking group. In other words, the final treatment with A did not result in retrospective revaluation of responding to X. The results are entirely consistent with the explanation for blocking put forward by for example, the Rescorla-Wagner model (1972).

The experiments used a new methodology to test predictions made by the comparator hypothesis (e.g. Miller and Schachtman, 1985) concerning retrospective revaluation. According to this hypothesis, the strength of the response to X during the test trials in each experiment will be inversely related to the associative strength of A at the time of testing. In each experiment, responding to A was more vigorous before Test 2 in the control than the blocking group which, according to the comparator hypothesis, should have resulted in stronger responding during X on this test by the blocking than the control group. In each experiment, however, the opposite outcome was recorded. The results from the three experiments thus pose a problem for the explanation of blocking provided by the comparator hypothesis. Blaisdell et al. (1999) have argued that in order to observe retrospective revaluation following blocking it is necessary to give many hundreds of extinction trials with the blocking cue after compound conditioning. While this may be true, it should be emphasised that this conclusion is not in keeping with the spirit or the detail of the comparator hypothesis,

especially as far as the present experiments are concerned. Once the extinction trials with A during Stage 3 in the blocking group have resulted in a weaker response than that resulting from the reinforced trials with A in the control group, the hypothesis unequivocally predicts that the outcome of Test 2 will be the opposite to that of Test 1.

Thus far I have examined the present results from the perspective of the comparator hypothesis put forward by Miller and Matzel (1988), but this hypothesis has since been developed into the Extended Comparator Hypothesis (Denniston, Savastano, & Miller, 2001), and there is also a Sometimes Competing Retrieval version of the hypothesis (Stout & Miller, 2007). The principal difference between the newer versions of this model and the original one is that Links 2 and 3 in Figure 1.1 (p27) can be influenced by second-order and third-order comparator processes. As far as second-order processes are concerned, the effectiveness of the X-A association in Link 2 of Figure 1.1 will be reduced by a function of the product of the strength of an X-context and a context-A association. Similarly, the effectiveness of the A-US association in Link 3 will be reduced by a function of the product of an A-context and a context-US association. The strength of each of these four second-order associations should not differ between the two groups. As a consequence, second-order comparator processes should not alter qualitatively the predictions that were derived from the original comparator hypothesis concerning the test trials with X. Second-order processes will, however, reduce the magnitude of the predicted influence of first-order comparator processes on responding to X.¹

¹ In addition to A, the context might also be conceived as being a first-order comparator for X, with A acting as a second-order comparator. However, Savastano et al. (2003) have argued that the salience of the context will be relatively low and because there are protracted periods when the context is presented in the absence of the US, its associative strength will be low relative to A, B or X. As a consequence, the influence of the context as a first-order comparator stimulus will be modest and not affect qualitatively the predictions that have already been derived.

Turning now to third-order comparator processes, these will exert an influence on the role played by the context-US association in second-order comparator processes. The strength of this association will be reduced by a function of the product of the context-B and the B-US associations. Consider the second test with X in the blocking group. At the time of this test, the first-order A-US association in Link 3 of Figure 1 will be close to zero, because of the extinction trials in Stage 3. The second-order comparator process for this link will weaken further the effectiveness of the A-US association. However, because B will have high associative strength its role in the third-order comparator process will be to weaken the second-order process. In other words, once account is taken of third-order comparator processes, the prediction concerning the outcome of the second test with the blocking group is much the same as that made by the original comparator hypothesis: the response to X will be strong. In contrast, because the strength of the B-US association can be assumed to be close to zero at the time of the second test in the control group, the third-order comparator process can be ignored in this group, which means performance during X will be weakened by the second-order comparator process. Thus the A-US association, which will be close to asymptotic strength because of the Stage-3 training, will be diminished to some extent by the second-order comparator process, but this effect will be slight because the context-US association on which it is based will be weak. Accordingly, despite the influence of third-order comparator processes, the comparator hypothesis predicts that the effectiveness of the A-US association will be greater in the control than the blocking group, and that responding during X will be weaker in the former than the latter. The fact that the opposite outcome was observed indicates that even the most complex version of the comparator hypothesis is unable to explain the results reported here.

Following the development of the comparator hypothesis, other theories were proposed which also predict that the properties of a blocked cue might be affected by subsequent training with the blocking stimulus (Van Hamme & Wasserman, 1994; Dickinson & Burke, 1996). However, in contrast to the comparator hypothesis, these theories are based on the same fundamental assumption as the Rescorla-Wagner (1972) model that stimuli compete for a limited pool of associative strength. Indeed, according to Van Hamme and Wasserman, retrospective revaluation effects can be explained with a simple modification to the Rescorla-Wagner equation. Suppose that animals receive conditioning with A+ and then AX+ before extinction trials with A. Van Hamme and Wasserman suggested that the acquisition of associative strength by A and X during compound conditioning, and the loss of associative strength by A during extinction, will be governed by the Rescorla-Wagner equation. Their novel proposal was that during extinction training with A, the associative strength of X will also be modified according to this equation, because X had previously been paired with A. However, because X is not physically presented during this stage, the value of α associated with this stimulus will be negative. Thus the change in the associative strength of X will be in the opposite direction to that of A. If A is presented without the US, X will gain associative strength as A loses it. Conversely, if A is paired with the US, then X will lose associative strength as A gains it. Dickinson and Burke developed a similar explanation, but it was couched in terms of Wagner's (1981) theory. In addition, they argued that learning about X on trials when A is presented by itself would take place only if there was a strong association between these stimuli.

Although both theories predict that the Stage-3 treatment given in Experiments 1 to 3 should result in X gaining associative strength in the blocking group, and losing it in the control group, it is not clear that they predict, as the comparator hypothesis

does, that the second test will necessarily reveal a stronger response to X in the blocking than the control group. Conceivably, the negative learning rate parameter for absent stimuli is relatively low, in which case the difference between the two groups on the first test should be diminished, but not reversed for the second test. Thus the failure to find a stronger response in the blocking than the control group during the second test with X need not be taken as evidence against these theories. A further reason why the present results may not pose a serious challenge to these theories can be based on the claim by Dickinson and Burke (1996) that effective retrospective revaluation depends upon the existence of strong within-compound associations. There are two reasons why these associations may not have been particularly strong in the present experiments. On the one hand, Freberg (1979, cited in Rescorla, 1981) has shown that preexposure to one element of a compound can disrupt the development of within-compound associations, which makes it possible that in each experiment the initial conditioning with A resulted in the subsequent formation of a weak A-X association (but see Balleine, Espinet & González, 2005). On the other hand, the independent presentations of A in Stage 3 of each experiment, and in Stage 2 of Experiments 2 and 3, may have weakened the A-X association formed during compound conditioning (e.g. Rescorla & Freberg, 1978; but see Esber, Pearce & Haselgrove, in press).

If the A-X association does not form, the theories of Van Hamme and Wasserman (1994) and Dickinson and Burke (1996) predict that retrospective revaluation will not occur, as A will not activate a representation of X when it is presented in extinction during Stage 3. In support of this proposal, Dickinson and Burke have shown with humans that retrospective revaluation effects are not obtained in the absence of within-compound associations (see also Melchers, Lachnit &

Shanks, 2006). If, however, the A-X association is formed but weakened by presentations of A alone, then on at least the initial extinction trials with A, a representation of X will be activated, allowing an increment in the associative strength of this stimulus. Hence, in this case a retrospective revaluation effect would be expected on test. The comparator hypothesis cannot explain the results of Experiments 1 to 3 by appealing to either the prevention of the X-A association or the weakening of this association. If the X-A association is prevented by the initial conditioning with A, blocking will not occur. However, if the X-A association forms and is then weakened by subsequent extinction trials with A, the combined influence of this weak association and the weak A-US association should result in a particularly strong recovery from blocking effect being observed on test.

The failure to observe retrospective revaluation following blocking is consistent with the results reported by Holland (1999), Rauhut et al., (2000) and by Miller, Schachtman and Matzel (1988, cited in Blaisdell et al., 1999). These results were all obtained with rats, but a similar failure to find a reversal of blocking by retrospective revaluation has also been reported using pigeons by Rescorla and Durlach (1981, p91-93). In contrast to these findings, and those reported here, Blaisdell et al. were able to observe a recovery from blocking after nonreinforced exposure to the blocking stimulus. There are a number of differences between the method adopted by Blaisdell et al. and that adopted for the present studies, which makes it difficult to explain why their findings were not replicated here. First, Blaisdell et al. used aversive conditioning with 12 A+ trials and 4 AX+ trials whereas Experiments 1, 2 and 3 involved appetitive conditioning and at least 120 A+ trials and at least 32 AX+ trials. Second, conditioning took place in a different context to the one where the extinction trials with A, and the test with X took place. The same

apparatus was used for all phases of each of the three experiments reported here. It is conceivable that if the design of these experiments had more closely matched that of Blaisdell et al. then an effect of retrospective revaluation on blocking might have been found. However, the principal purpose of the experiments was not to identify the circumstances under which retrospective revaluation on blocking can be found. Rather, it was to test a specific prediction of the comparator hypothesis by examining whether the effects on X of two different types of training, A+ then AX+ or A- then AX+, can be reversed by reversing the significance of A. The failure to replicate the results of Blaisdell et al. (1999) does not affect at all the conclusions drawn from these experiments, namely, that responding during X was unaffected by the reversal training with A.

Matzel, Shuster and Miller (1987) report that after conditioning with AX+, responding to X was enhanced by subsequent A- trials, but not affected by A+ trials. The implication of this finding for the present experiments is that the reinforced trials with A during Stage 3 in the control group may not have been ideal for revealing retrospective revaluation effects with blocking. Whether or not this is the case, the treatments in Stage 3 were effective in producing stronger responding to A in the control than the blocking group. As just noted, such an outcome according to the comparator hypothesis should have revealed a complementary pattern of results with X during the final test, yet the opposite was observed.

The retrospective revaluation effect brought about by the A- trials in the above study by Matzel et al. (1987) has been reported on a number of occasions in overshadowing studies with animals (Balleine et al., 2005; Kaufman & Bolles, 1981; Liljeholm & Balleine, 2006; Matzel, Schachtman & Miller, 1985; Miller, Barnett & Grahame, 1992). If retrospective revaluation is effective in these circumstances, the

question is then raised as to why it is less successful with blocking. Perhaps, as noted above, the necessity of presenting the blocking cue separately from the blocked cue makes it difficult for associations to develop between the stimuli. In the absence of these associations, Dickinson and Burke (1996) have argued that retrospective revaluation is unlikely to take place.

Previous studies that have looked for evidence of retrospective revaluation have relied on extinction training with the blocking cue to test for retrospective revaluation following blocking. In the novel design reported here, whilst the blocking group initially received reinforced presentations of the blocking cue, A, the control group received nonreinforced presentations of this cue. The reversal of this training following blocking meant that as well as giving extinction training with A in the blocking group, reinforced presentations of this cue were given in the control group. Revaluing A in both groups allowed the predictions of the comparator hypothesis to be tested, but avoided the difficult question of how many extinction trials to give. Therefore although further research may be required to determine the precise conditions that give rise to retrospective revaluation in blocking, the present results show clearly that blocking does not depend upon the associative strength of A being high at the time when X is tested. On this basis, it must be concluded that at least in certain circumstances, blocking is a consequence of a failure by a stimulus to acquire associative strength.

3. The Role of Attention in Discrimination Learning

Introduction

The three experiments reported in Chapter 2 tested two accounts of the blocking effect, in an attempt to determine the extent to which animals learn about irrelevant stimuli. The results of each experiment suggested that blocking arises from competition between stimuli for a limited pool of associative strength (e.g. Rescorla & Wagner, 1972) rather than a failure to express an association that has been acquired (e.g. Miller & Matzel, 1988). The implication of these results is that little is learned about irrelevant stimuli because they gain less associative strength than stimuli that are relevant.

In contrast to the assumptions of the Rescorla-Wagner (1972) model, the theories of Mackintosh (1975a) and Pearce and Hall (1980) propose that stimuli compete for attention rather than associative strength, and thus irrelevant stimuli are not learned about because they fail to gain attention. These two theories are as capable of explaining the results of Experiments 1, 2 and 3 as the Rescorla-Wagner model, and thus an alternative method is required to distinguish between them. The experiments reported in this chapter are based on the simple discrimination training given in a relative validity task. As detailed in Chapter 1, this task provides convincing evidence that subjects learn about stimuli that are relevant to the particular outcome that follows them at the expense of those that are irrelevant to that outcome. Owing to the difficulties that the Pearce-Hall model encounters with effects related to relative validity (see Chapter 1), in the present chapter I shall focus on Mackintosh's theory, which has proved to be particularly successful in accounting for the relative validity effect and related findings.

Wagner et al. (1968) were the first to report the relative validity effect. That is, if animals were trained initially with the true discrimination AX+ BX-, conditioned responding on a subsequent test of X alone was reduced relative to when AX and BX were each initially followed by food on 50% of their presentations (a pseudo discrimination). As described in Chapter 1, it follows from the theory of Mackintosh (1975a) that during true discrimination training, attention decreases to X because the stimuli A and B are more accurate predictors of reinforcement and nonreinforcement respectively. Pseudo discrimination training does not have such a profound effect on the associability of X because A, B and X all predict the outcome to the same extent.

A similar explanation can be applied to the IDS/EDS procedure, which involves true discriminations such as AX+ BX- and AY+ BY-, where stimuli A and B are from one dimension and X and Y are from another. A and B are accurate predictors of the outcome that follows each compound (signalling reinforcement and nonreinforcement respectively) and are therefore relevant to the discrimination. X and Y are inaccurate predictors of the outcome, being followed by each outcome on 50% of their presentations, and are therefore irrelevant. Mackintosh (1975a) proposed that this training will cause an increase in attention to the relevant stimuli A and B, which will generalise to similar stimuli. Stimuli from the same dimension are likely to be more similar to one another than stimuli from different dimensions, and thus a subsequent discrimination involving novel stimuli will be facilitated if the relevant stimuli are from the same dimension as A and B.

As discussed in Chapter 1, this prediction has been confirmed by a number of researchers using a variety of species, but the effect has not always been found. One reason for these discrepant results could be that the typical IDS/EDS procedure relies on generalisation occurring from previously relevant stimuli to novel stimuli on the

basis of their similarity. Pearce, Esber, George and Haselgrove (2008) devised a novel variation of the IDS/EDS method in an attempt to address this shortcoming. Using an autoshaping procedure, they trained pigeons on a number of true discriminations where each compound consisted of two squares that appeared side by side on a computer screen. One of these squares was filled with one of four plain colours (A, B, C or D) and the other was filled with one of four patterns (W, X, Y or Z). The true discriminations received are given in Figure 3.1. For a colour-relevant group the colours A, B, C and D signalled either the presence or the absence of food, and were therefore relevant to the solution of the discrimination. The patterns W, X, Y and Z were irrelevant, signalling the presence and absence of food equally. For a pattern-relevant group the patterns W, X, Y and Z were relevant, and the colours A, B, C and D were irrelevant.

Following this training, both groups received a test discrimination which consisted of reinforced presentations of the compound AY, and nonreinforced presentations of the compounds AW and CY. The compound AY was novel and consisted of one previously relevant element and one previously irrelevant element. This reinforced compound elicited a high level of responding from the onset of the test discrimination. The other two compounds involved in the discrimination (AW and CY) were familiar, having been reinforced for both groups during training. Consider first the discrimination between AY+ AW-, which is based on two patterns that were relevant to the pattern-relevant group during training. Pearce et al. (2008) observed that extinction to AW progressed more rapidly in the pattern-relevant group than in the colour-relevant group, indicating that the pattern-relevant group solved the AY+ AW- discrimination more rapidly than the colour-relevant group. This result suggests that discrimination training resulted in more attention being paid to patterns in the

pattern-relevant group than in the colour-relevant group, facilitating a subsequent discrimination based on these stimuli in the former group. The test discrimination AY+ CY- was based on two colours that were relevant for the colour-relevant group during training. If training had indeed increased attention to relevant stimuli, then the colour-relevant group would be expected to acquire the AY+ CY- discrimination more readily than the pattern-relevant group. However, responding in the presence of CY was found to extinguish equally rapidly in both groups.

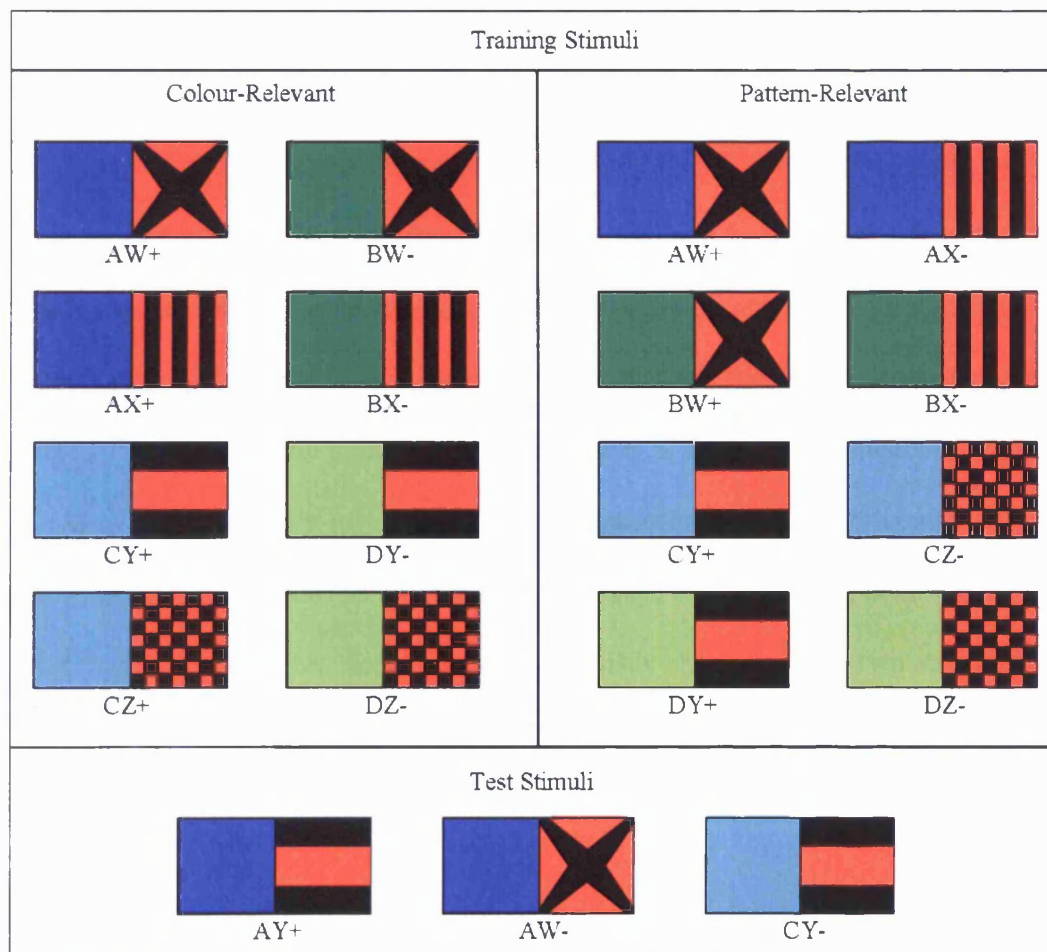


Figure 3.1. The stimuli that were used for the true discriminations and subsequent test discrimination given by Pearce et al. (2008).

These results suggest that the true discrimination training given by Pearce et al. (2008) influenced the attention paid to patterns, but had no effect on attention to colours. These findings are not fully compatible with theories of attention such as that proposed by Mackintosh (1975a), which predicts that attention to both dimensions should have been modified by the training given, but they cannot be explained purely by appealing to standard associative principles. If the rate of responding to the test compounds was determined simply by their individual overall associative strengths (e.g. Rescorla & Wagner, 1972) then responding to AY should be maintained at a high level during the test, whilst responding to AW and CY should decrease over the course of the test at a similar rate in both groups.

In summary, the novel design employed by Pearce et al. (2008) produced some evidence that attentional processes are involved in discrimination learning. This result was achieved without relying on generalisation of attention from training stimuli to entirely novel stimuli on test, a factor that has been identified as a possible cause of the mixed results produced by traditional IDS/EDS experiments. However, attention to stimuli from just one of the two dimensions used was influenced. For the two experiments reported in this chapter, the design used by Pearce et al. was modified in an attempt to demonstrate associability changes within two stimulus dimensions, and to test the generality of these effects by using two species of subjects; pigeons and rats.

Experiment 4

The design of Experiment 4 is presented in Figure 3.2. During training, two groups of pigeons received eight true discriminations. For a colour-relevant group four colours, C₁, C₂, C₃ and C₄, were relevant, with C₁ and C₂ consistently signalling

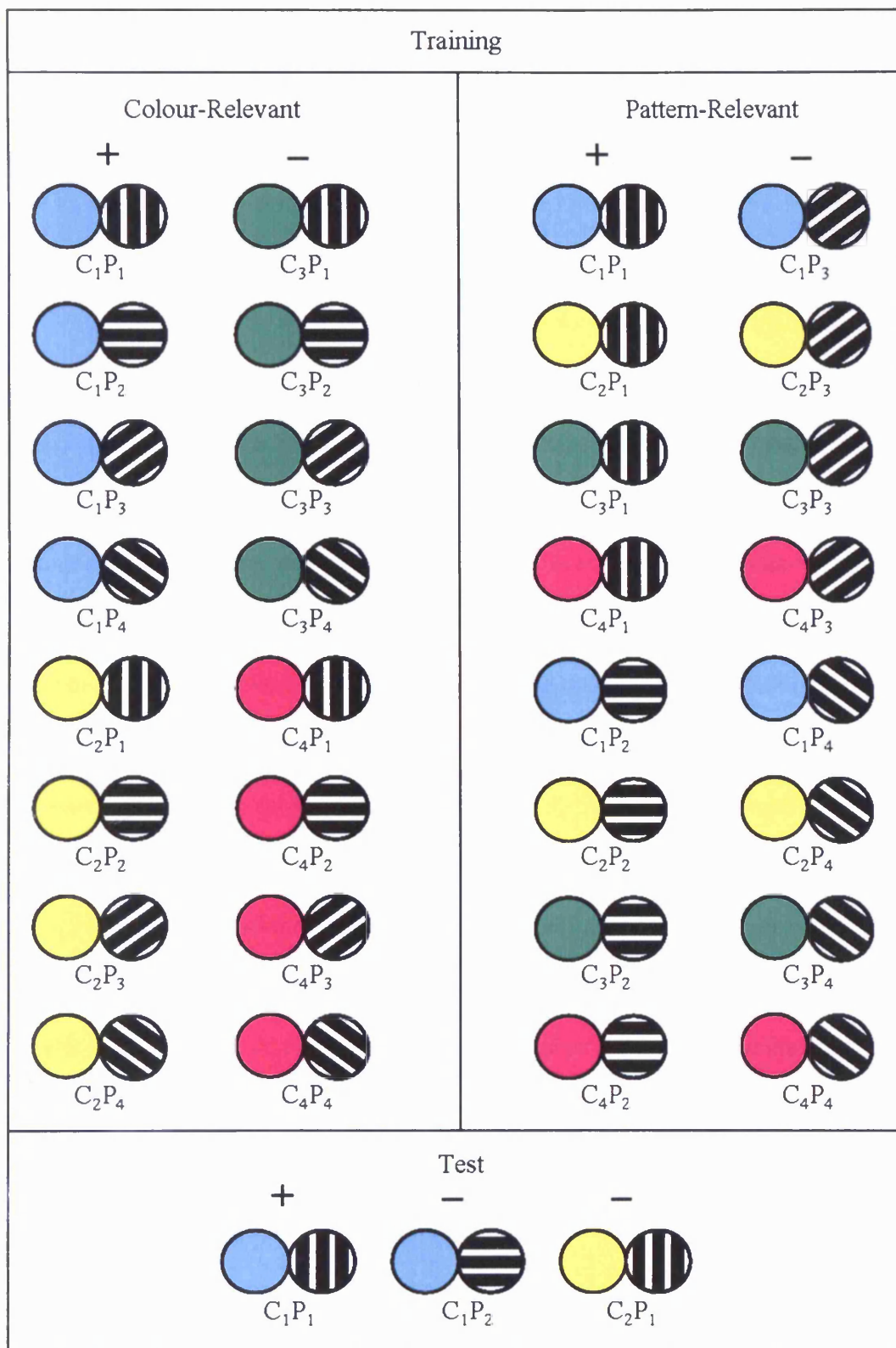


Figure 3.2. The stimuli that were used for the true discriminations and subsequent test discrimination received by the two groups in Experiment 4, for one of the counterbalanced conditions.

the presence of food and C₃ and C₄ consistently signalling the absence of food. The patterns P₁, P₂, P₃ and P₄ were irrelevant, signalling food and the absence of food equally. For a pattern-relevant group the patterns P₁ and P₂ consistently signalled food and P₃ and P₄ consistently signalled the absence of food. The colours C₁, C₂, C₃ and C₄ were irrelevant for this group.

From Figure 3.1, it can be seen that the test discrimination based on colours (AY+ CY-) that was given by Pearce et al. (2008) involved discriminating between light blue and dark blue. Such a test could therefore be construed as a brightness discrimination rather than a colour discrimination, which could explain why both the colour-relevant and pattern-relevant groups solved it at a comparable rate – brightness was not previously relevant for either group. To avoid this confound, the four colours used in Experiment 4 were yellow, cyan, green and magenta, which were matched for brightness. The patterns used in Experiment 4 also differed from those that Pearce et al. used. In their study subjects found the patterns difficult to discriminate, as indicated by slow acquisition of the training discriminations by the pattern-relevant group relative to the colour-relevant group. In Experiment 4, the patterns were simplified, such that each consisted of three black lines of the same width that were superimposed on a white circle. The patterns therefore differed only in the orientation of these lines (0°, 90°, 45° and -45°).

Following training, both groups received a test discrimination that involved three compounds. Including more training trial types than Pearce et al. (2008) allowed three compounds that had been reinforced for both groups during training to be presented on test. One of these compounds continued to be reinforced during the test discrimination and the other two were nonreinforced. This arrangement avoided the issue of generalisation from familiar to novel compounds, and thus constituted an

improvement on the test discrimination given by Pearce et al., where two familiar compounds were accompanied by a compound that had not been encountered during training.

If the training given resulted in the colour-relevant group attending preferentially to C_1 , C_2 , C_3 and C_4 , and the pattern-relevant group to P_1 , P_2 , P_3 and P_4 (e.g. Mackintosh, 1975a), responding should decrease at a different rate to the two nonreinforced compounds presented at test in these groups. As the discrimination between C_1P_1 and C_2P_1 is based on two colours that were relevant during training for the colour-relevant group, this group should learn the discrimination relatively more quickly than the pattern-relevant group, for whom these colours were irrelevant during training. Thus the rate of responding to C_2P_1 should decline more rapidly in the colour-relevant group than in the pattern-relevant group. If the pattern-relevant group had learnt to attend preferentially to P_1 , P_2 , P_3 and P_4 , the discrimination between C_1P_1 and C_1P_2 should be solved more readily in this group than in the colour-relevant group, as it is based on two patterns which were relevant to the pattern-relevant group during training, but irrelevant to the colour-relevant group. Thus the rate of responding to C_1P_2 should decline more rapidly in the pattern-relevant group than in the colour-relevant group. Although Pearce et al. (2008) found that their pattern-relevant group acquired the test discrimination based on patterns more rapidly than the colour-relevant group, they observed no difference between the two groups in the rate at which responding extinguished to the compound where the distinctive cue was the colour. They inferred from this result that attention to colour had not been influenced differentially in the two groups during training. Having modified their design, in Experiment 4 an effect of group was expected for responding to both the

compound where the distinctive cue was the pattern, and to the compound where the distinctive cue was the colour.

In a final modification to Pearce et al.'s (2008) design, test trials which involved presenting each colour and pattern individually were included towards the end of the training phase. The aim of these trials was to test the associative strength of stimuli that had been consistently reinforced, consistently nonreinforced and irrelevant in the two groups. If the associative strengths of patterns and colours within each of these three categories are found to be comparable, then any differences between the two groups that emerge on test cannot be interpreted in these terms.

Method

Subjects. The subjects were 32 experimentally naïve adult homing pigeons. The pigeons were housed in pairs and had free access to water and grit in their home cages. They were maintained at 80% of their free-feeding weights by being fed a restricted amount of food after each experimental session. They were maintained in a lightproof room in which the lights were on for 14.5 hr each day.

Apparatus. The experimental apparatus consisted of eight pigeon test chambers (30.0 x 33.0 x 35.0 cm). Each contained an 8.3-cm-high x 6.3-cm-wide clear acrylic panel, which was hinged at the top. Pecks on the panel were detected by a reed relay that was operated whenever a magnet attached to its lower edge was displaced by a distance greater than 1 mm. The midpoint of the panel was 24 cm above the floor of the chamber. A colour thin film transistor TV with a 15.5 x 8.7-cm screen was located 2.0 cm behind the acrylic panel. Food was delivered by operating a grain feeder (Colbourn Instruments, Lehigh Valley, PA) with an opening that measured 4.6 cm x 5.4 cm located in the same wall as the response key. The midpoint

of the opening was 9.0 cm above the chamber floor and 7.0 cm to the left of the midline of the wall. The feeder was illuminated whenever grain was made available. The chambers were permanently lit during all experimental sessions by a 2.8-W bulb, operated at 24 V, located in the centre of the ceiling of the chamber. Risc PC microcomputers (Acorn Computers Ltd., Cambridge, England), which were programmed in Arachnid (Paul Fray Ltd., Cambridge, England), were used for the control of events, recording of responses, and generation of stimuli on the TV screens.

Stimuli. The stimuli were presented on the TV screen, which was otherwise black. The stimuli consisted of 2 adjacent circles, each 2.4 cm in diameter. The point at which the circles joined was located at the centre of the TV screen. One of the circles was filled with one of four plain colours, and the other was filled with one of four patterns. On half of the trials, the coloured circle appeared on the left, on the other half it appeared on the right. The four colours were cyan, yellow, green and magenta, and the four patterns were three black vertical bars, each 3 mm wide, separated by white bars of the same width. For each pattern the orientation of the bars with respect to the top of the TV was different; either 0°, 45°, 90° or -45°.

The stimuli were counterbalanced in the following way. For half of the subjects C₁, C₂, C₃ and C₄ represented cyan, yellow, green and magenta respectively, and P₁, P₂, P₃ and P₄ represented patterns with stripes of orientation 0°, 90°, 45°, or -45°. For the other half, C₁, C₂, C₃ and C₄ represented yellow, cyan, magenta and green respectively, and P₁, P₂, P₃ and P₄ represented patterns with stripes of orientation 90°, 0°, -45°, or 45° respectively.

In the colour-relevant group, each of the four colours served as relevant cues signalling either the presence or absence of food, and the four patterns served as irrelevant cues, signalling the presence and absence of food equally. In the pattern-

relevant group, the four patterns served as the relevant cues, and the four colours were the irrelevant cues.

Procedure. The subjects first received eight sessions in which they were trained to eat food whenever the hopper was operated. They were then given five sessions of autoshaping in which a white circle with a diameter of 2.4 cm was presented in the middle of the TV screen for 10 sec. There were 45 trials in a session, the mean interval between the start of each trial was 60 s (range = 35-85 sec), and food was made available in the hopper for 4 s whenever the white circle was removed from the TV screen.

Session 1 of training began on the day after the final session of autoshaping. During each of the 20 sessions of training, the two groups received discrimination training with the 16 trial types given in Figure 3.2. There were 64 trials in each session: each trial type was presented twice with the coloured circle on the left, and twice with the coloured circle on the right. The following details applied to all stages of this experiment. Each stimulus was presented for 10 sec, and the mean inter-trial interval was 60 sec (range = 35-85 sec). The trial types were presented in a random order with the constraint that no more than three reinforced or three nonreinforced trials could occur in succession.

On the eighteenth session of training, all subjects received 64 training trials, as in each of the other sessions. In addition, these trials were intermixed with 16 nonreinforced trials on which only one circle (with diameter 2.4 cm), which contained either a colour or a pattern, was presented on the screen. Each of the four colours and four patterns was presented individually on two different trials in this session; once where the left-hand circle of the training stimuli appeared, and once where the right-hand circle appeared.

On the day following session 20 of training, both groups received the first session of the test discrimination. There were 10 sessions in the test phase, during which all animals received a discrimination involving three trial types that had been reinforced during training: C_1P_1+ C_1P_2- C_2P_1- . There were 40 trials in each session of the test discrimination, consisting of 20 reinforced presentations of C_1P_1 , 10 nonreinforced presentations of C_1P_2 and 10 nonreinforced presentations of C_2P_1 .

Results

A Type-1 error rate of $p < .05$ was adopted for all of the statistical tests. The mean rate of responding during presentations of the eight reinforced compounds during training was calculated for each bird on each session, and the same was done for the eight nonreinforced compounds. These data are presented for both groups in Figure 3.3. From this figure it appears that the colour-relevant group acquired the discrimination between reinforced and nonreinforced trial types more readily than the pattern-relevant group, but that by the end of training the two groups were responding at a similarly high rate during reinforced trial types, and a similarly low rate during nonreinforced trial types.

A three-way analysis of variance (ANOVA) of individual mean response rates during presentations of each trial type was conducted, with the factors of group (colour-relevant or pattern-relevant), trial type (reinforced and nonreinforced) and session, for the 20 sessions of training. The results from this ANOVA revealed a significant effect of session, $F(19, 570) = 7.62$, $MSE = 14.01$, and trial type, $F(1, 30) = 291.92$, $MSE = 663.76$, and significant Group x Trial Type, $F(1, 30) = 5.40$, $MSE = 663.76$, Group x Session, $F(19, 570) = 3.47$, $MSE = 14.07$, Trial Type x Session,

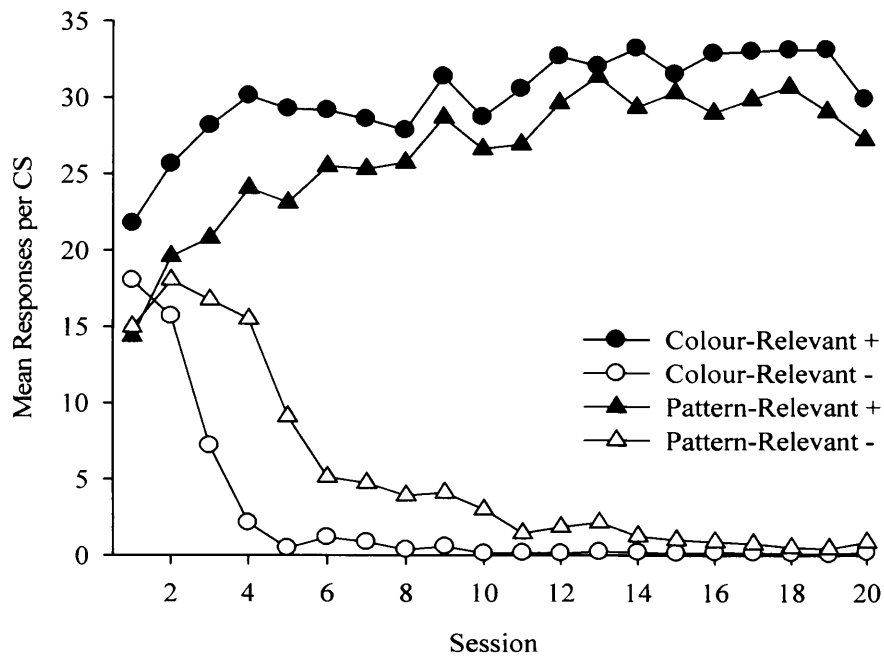


Figure 3.3. The mean rate of responding during the CS by the two groups in Experiment 4 during reinforced and nonreinforced trials of the training discrimination.

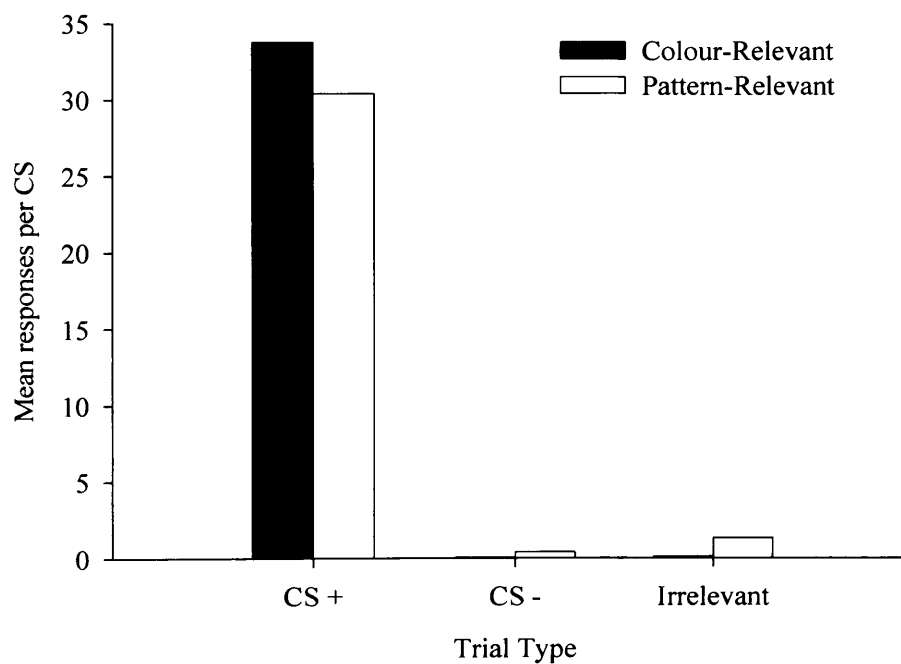


Figure 3.4. The mean rate of responding during Session 18 of training in Experiment 4 to individual elements that had been reinforced (CS+), nonreinforced (CS-) and irrelevant during training.

$F(19, 570) = 75.86$, $MSE = 16.19$, and Group x Trial Type x Session, $F(19, 570) = 5.69$, $MSE = 16.19$, interactions. There was no significant effect of group, $F < 1$.

The three-way interaction was analysed using simple main effects tests, which confirmed that the two groups acquired the discrimination at different rates. There was a significant difference between responding during the two trial types from Session 2 onwards in the colour-relevant group, $F_s(1, 600) > 16.28$, $MSE = 48.57$, and from Session 4 onwards in the pattern-relevant group, $F_s(1, 600) > 12.13$, $MSE = 48.57$. A further simple main effects test revealed that there were differences between the two groups in the rate of responding during reinforced trials on Sessions 1 to 5, $F_s(1, 1200) > 5.17$, $MSE = 56.38$, and during nonreinforced trials on Sessions 3, 4 and 5, $F_s(1, 1200) > 10.59$, $MSE = 56.38$.

Session 18 of training contained trials on which each of the coloured and patterned circles that were involved in training were presented individually. Thus far, for the colour-relevant group, two colours had been consistently reinforced (C_1 and C_2), two had been consistently nonreinforced (C_3 and C_4) and four patterns had been reinforced on 50% of the trials on which they were present, that is, they were irrelevant (P_1 , P_2 , P_3 and P_4). For the pattern-relevant group P_1 and P_2 had been consistently reinforced, P_3 and P_4 consistently nonreinforced and C_1 , C_2 , C_3 and C_4 had been irrelevant. For trials on which an individual colour or pattern was presented, the mean rate of responding during consistently reinforced stimuli was calculated for both groups, and the same was done for consistently nonreinforced stimuli and irrelevant stimuli.

The group means derived from these data are presented in Figure 3.4. From this figure it is evident that both groups responded at a high rate during the presentations of stimuli that had been consistently reinforced, and responded

minimally to those that had been consistently nonreinforced, and those that had been irrelevant. These observations were confirmed by a two-way ANOVA of individual mean responses made during presentations of each of these trials, with the factors of group (colour-relevant or pattern-relevant) and stimulus (CS+, CS- and irrelevant). This analysis revealed a significant effect of stimulus, $F(2, 60) = 283.28$, $MSE = 37.65$, but no significant effect of group, $F < 1$, and no significant Group x Stimulus interaction, $F(2, 60) = 1.26$, $MSE = 37.65$. Subsequent Bonferroni corrected pairwise comparisons revealed that the two groups responded at a significantly higher rate during reinforced trial types than during nonreinforced trial types, $t(31) = 17.16$, and irrelevant trial types, $t(31) = 16.11$, but at a similar rate during nonreinforced and irrelevant trial types $t(31) = 2.09$.

The mean number of responses during presentations of the reinforced compound C₁P₁ across the 10 sessions of the test phase was 32.46 for the colour-relevant group and 26.05 for the pattern-relevant group. A two-way ANOVA of individual mean number of responses made in the presence of this compound, with the factors of group (colour-relevant or pattern-relevant) and session, revealed that there was no effect of group, $F(1, 30) = 2.69$, $MSE = 1222.48$, session, $F(9, 270) = 1.49$, $MSE = 25.29$, or Group x Session interaction, $F < 1$. The lack of difference between responding to the reinforced compound in the two groups allows a meaningful comparison of the rate at which responding to the other nonreinforced test compounds extinguished.

In order to simplify the comparison of the rate at which the colour-relevant and pattern-relevant groups acquired the discriminations during the test discrimination, discrimination ratios were calculated for each subject on every session. These ratios were of the form $Y / (Y+X)$, where X represents the mean

duration of responding during presentations of the reinforced compound C_1P_1 on each session, and Y represents the mean duration of responding during presentations of one of the nonreinforced compounds (C_1P_2 or C_2P_1). A ratio of 0.5 thus indicates a failure to discriminate between reinforced and nonreinforced trials, whereas a ratio of 0.0 indicates a perfect discrimination between these trials. The mean discrimination ratios for the component of the test discrimination that was based on patterns ($C_1P_1 + C_1P_2$) are shown in the upper panel of Figure 3.5, and the ratios for the component that was based on colours ($C_1P_1 + C_2P_1$) are shown in the lower panel of this figure.

Inspection of the upper panel of Figure 3.5 suggests that the pattern-relevant group acquired the discrimination for which patterns were relevant more rapidly than the colour-relevant group. Furthermore, the colour-relevant group had not acquired this discrimination by the end of training. A two-way ANOVA was conducted on individual mean discrimination ratios during each session of the test phase with the factors of group (colour-relevant or pattern-relevant) and session. This analysis revealed a significant effect of group, $F(1, 30) = 58.71$, $MSE = 0.06$, and Session, $F(9, 270) = 31.08$, $MSE = 0.01$, and a significant Group x Session interaction, $F(9, 270) = 24.64$, $MSE = 0.01$. This interaction was analysed using simple main effects tests, which confirmed that there was a significant effect of group from Session 4 onwards, $F_s(1, 300) > 16.77$, $MSE = 0.01$.

Inspection of the lower panel of Figure 3.5 suggests that the colour-relevant group acquired the discrimination for which colours were relevant more rapidly than the pattern-relevant group, although by the end of training both groups had acquired the discrimination to the same extent. These observations were confirmed by a two-way ANOVA conducted on individual mean discrimination ratios during each session

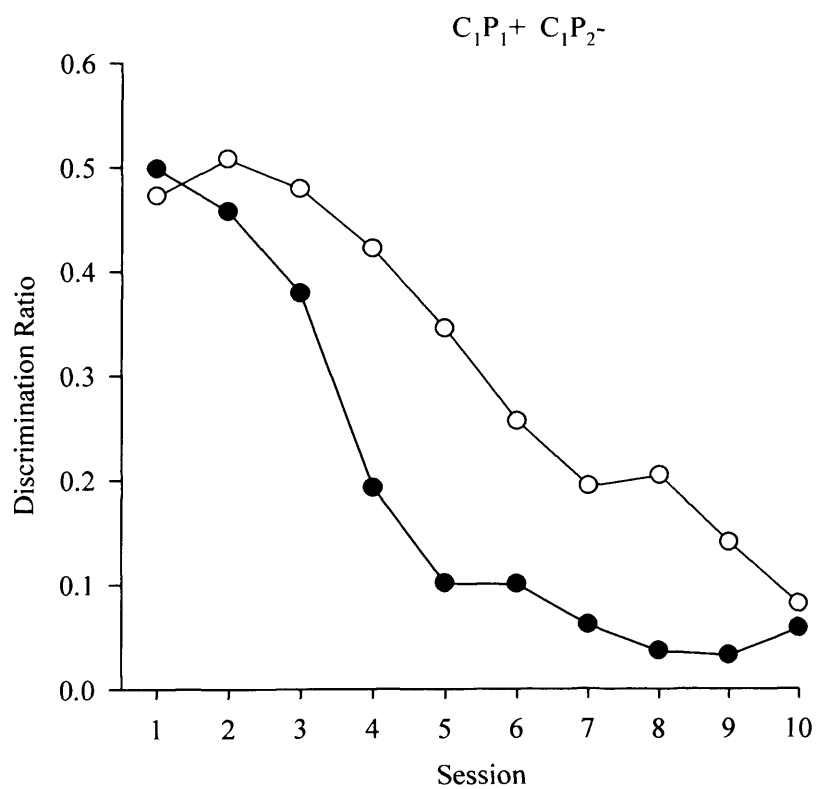
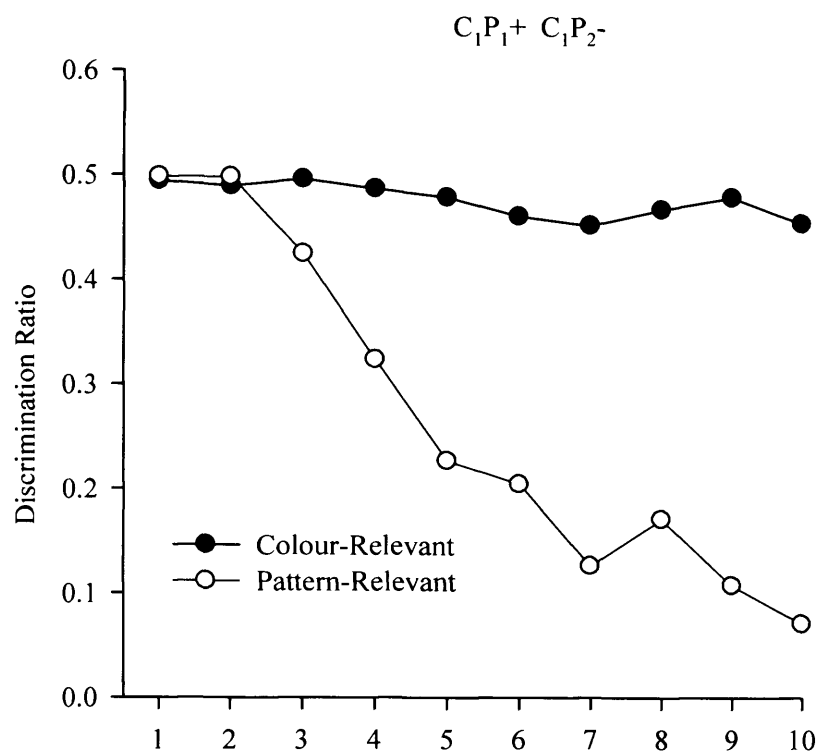


Figure 3.5. Mean discrimination ratios for the two groups for each session of the test stage during Experiment 4, for the discrimination where pattern was relevant (upper panel) and the discrimination where colour was relevant (lower panel).

of the test phase with the factors of group (colour-relevant or pattern-relevant) and session. This analysis revealed a significant effect of group, $F(1, 30) = 23.58$, $MSE = 0.05$, and Session, $F(9, 270) = 78.39$, $MSE = 0.01$, and a significant Group x Session interaction, $F(9, 270) = 6.92$, $MSE = 0.01$. The interaction was analysed using simple main effects tests, which confirmed that there was a significant effect of group from Session 3 to Session 9 inclusive, $F_s(1, 300) > 5.76$, $MSE = 0.01$.

Discussion

Experiment 4 confirmed the finding reported by Pearce et al. (2008) that when patterns were trained as relevant during discrimination training and colours were irrelevant, the subsequent learning of a test discrimination based on patterns was facilitated relative to when patterns were initially irrelevant. These results are inconsistent with the predictions of the Rescorla-Wagner (1972) model. When the individual colours and patterns were tested towards the end of training, the colour-relevant and pattern-relevant groups responded at a similarly high rate to those elements that had been consistently reinforced during training, and at a similarly low rate to those elements that had been irrelevant during training. During the test discrimination, each compound presented comprised one previously reinforced element and one previously irrelevant element, and hence the associative strength of each compound in both groups should have been comparable. It then follows from the Rescorla-Wagner model that responding to the two nonreinforced compounds should have extinguished at a comparable rate in the colour-relevant and pattern-relevant groups, and thus both components of the test discrimination should have been acquired at similar rates in the two groups.

The results of Experiment 4 also rule out an alternative non-attentional explanation for the IDS/EDS effect that has been proposed by Hall (1991). Consider an IDS/EDS task that involves the true discriminations $AX^+ BX^- AY^+ BY^-$, where A and B are relevant to the discrimination, and X and Y are irrelevant. In this discrimination, the relevant cues A and B signal different outcomes (reinforcement and nonreinforcement respectively) whereas the irrelevant cues X and Y signal the same outcome (reinforcement on 50% of trials). There is evidence that increased generalisation occurs between stimuli that signal the same outcome (e.g. Honey & Hall, 1989). Hall (1991) suggested that rather than paying less attention to X and Y than to A and B, it could be that animals treat stimuli from the irrelevant dimension as equivalent, making them more difficult to distinguish than those stimuli that belong to the relevant dimension. The results of the experiment by Pearce et al. (2008) and of Experiment 4 cannot be explained in terms of this ‘acquired equivalence’ account, because the relevant stimuli presented at test signalled the same outcome during training. Consider the test discrimination given in Experiment 4: $C_1P_1^+ C_1P_2^- C_2P_1^-$. In the colour-relevant group, for example, the irrelevant stimuli P_1 and P_2 both signalled reinforcement on 50% of trials during training, and thus this group should find the discrimination based on these stimuli ($C_1P_1^+ C_1P_2^-$) difficult. However, the relevant stimuli C_1 and C_2 were both followed by reinforcement during training, and thus on the basis of Hall’s (1991) account, there is no reason why the discrimination based on these stimuli ($C_1P_1^+ C_2P_1^-$) should be solved more readily than that based on the irrelevant stimuli.

The results of Pearce et al.’s (2008) experiment and Experiment 4 can, however, be explained in terms of Mackintosh’s (1975a) theory of attention by assuming that the associability of patterns increased when they were relevant during

training as these stimuli were the best predictors of reinforcement and nonreinforcement. In contrast to the findings of Pearce et al., Experiment 4 provided evidence that the associability of colour stimuli can be similarly affected. That is, if colours were relevant during training, the test discrimination based on colours was facilitated compared to when patterns had initially been relevant. In the introduction to this chapter it was suggested that Pearce et al. failed to observe this effect due to factors such as the particular colours they used, the complexity of their pattern stimuli and the use of an unfamiliar compound on test. Steps were taken to eliminate each of these potential confounds in Experiment 4, which allowed evidence for a change in the associabilities of the colour stimuli to be observed.

Although it has been inferred that the associability of colours was affected by the training given in Experiment 4, it should be acknowledged that changes in the associability of patterns were much more pronounced. One reason for this finding could be that the plain colours were simply more salient than the pattern stimuli. It has been suggested (e.g. Le Pelley, 2004) that it is difficult to modify the associability of a stimulus when it has a high starting value. Indeed, evidence that colours initially had higher associability than the patterns is provided by the fact that the colour-relevant group acquired their training discriminations significantly more rapidly than pattern-relevant group. Nevertheless, the novel design used in Experiment 4 proved to be an effective method for revealing associability changes to both colours and patterns during true discrimination learning in pigeons. In order to test the generality of these findings the same basic design was used in Experiment 4, but the subjects used were rats.

Experiment 5

The aim of Experiment 5 was to demonstrate further the effectiveness of the novel method for assessing attentional processes in discrimination learning that was used in Experiment 4. Of interest was whether similar effects to those observed in pigeons could also be found in rats.

A number of variations on the traditional IDS/EDS procedure have been used to demonstrate associability changes in rats. Shepp and Eimas (1964) presented rats with a two-choice simultaneous object discrimination, for which the dimension of shape or orientation of stripes on the shape was relevant. Each of the two objects presented on a given trial was placed over a food well, one of which was baited, and the rats learned to displace the appropriate object to gain reward. Subjects then received either an ID or ED shift involving different stimuli from the same two dimensions. In an experiment by Birrell and Brown (2000), rats were trained to dig for food reward in small bowls. They were then presented with two bowls, one of which was baited. The bowls could vary according to their odour, their texture or the medium of the digging material they contained (e.g. styrofoam or shredded paper). Rats learned that one of these dimensions was relevant, that is, it signalled which was the baited bowl, and another was irrelevant. They then received novel exemplars from each of these dimensions in an ID or ED shift. Both of these experiments were successful in demonstrating an ID shift advantage, but the results can be explained in terms of the acquired equivalence account proposed by Hall (1991) that was discussed in the preceding section.

Duffaud, Killcross and George (2007) devised a novel procedure for assessing attentional processes in discrimination learning in rats that used stimuli from two different modalities. The design of their experiment is presented in Table 3.1, in

which A, B C and D are auditory cues and W, X, Y and Z are visual cues. R1 and R2 were pressing a lever on the left or pressing a lever on the right.

Table 3.1. Design of the Duffaud, Killcross and George (2007) Experiment.

Group	Phase 1		Phase 2	Test
Auditory-Relevant	AX → R1	BX → R2		
	AY → R1	BY → R2	CW → R1	DW → ?
Visual-Relevant	AX → R1	AY → R2	DZ → R2	CZ → ?
	BX → R1	BY → R2		

In Phase 1 either the auditory or the visual component of the compound was relevant to the solution of the discrimination. For example, for auditory-relevant animals, R1 was reinforced during trials on which A was presented, regardless of whether X or Y was present, and R2 was reinforced during trials on which B was presented. In the visual-relevant group, R1 was reinforced during trials with X, and R2 reinforced during trials with Y, regardless of whether these stimuli were accompanied by A or B. By the end of Phase 1, all animals had learnt the discrimination and were producing more responses on the reinforced lever than the nonreinforced lever. Following Phase 1, both groups received three sessions during which two compounds comprising novel auditory and visual cues were presented. R1 was reinforced during presentations of CW, and R2 was reinforced during presentations of DZ. As only two compounds were presented, all stimuli and thus both stimulus dimensions were relevant to the solution of the discrimination, and both groups learned to respond more on the lever that was reinforced in each case than on the lever that was nonreinforced.

The prediction was that during Phase 1, animals would learn to attend to stimuli from the dimension that was relevant to the discrimination, at the expense of stimuli from the irrelevant dimension. In turn, this change in attention would aid subsequent discriminations involving stimuli from the relevant dimension. Consider the presentation of the compounds CW and DZ in Phase 2. For the auditory-relevant group, C and D belong to the dimension that was relevant in Phase 1, and thus rats might learn that if they press R1 in the presence of C and R2 in the presence of D, they will receive reinforcement, paying little attention to the accompanying stimuli.

On the final session of Phase 2, animals received probe test trials, one with the compound DW, and one with the compound CZ. If the auditory-relevant group had indeed learnt a particularly strong association between C and R1 and D and R2, on the probe test of CZ they would press R1, and on the test of DW they would press R2. In contrast, if the visual-relevant group had learnt to attend preferentially to visual stimuli, in Phase 2 they would associate W with R1 on CW trials, and Z with R2, at the expense of C and D. Thus, on the subsequent probe trials, they would press R1 in the presence of DW and R2 in the presence of CZ. These predictions were confirmed, providing support for the suggestion that animals paid more attention to stimuli from the relevant dimension in Phase 1 than to stimuli from the irrelevant dimension, meaning that subsequently they learnt more about stimuli from the previously relevant dimension than about those from the previously irrelevant dimension.

Duffaud et al. (2007) argued that one of the strengths of their design over the traditional IDS/EDS procedure is the inclusion of Phase 2 which ensures that the stimuli involved in the test discrimination are familiar. Assuming that attention increases to relevant stimuli during Phase 1 and there is generalisation to stimuli from the same dimension in Phase 2, the relevant stimuli in Phase 2 will be better

predictors of the outcome than the irrelevant stimuli. Attention to these stimuli will therefore increase further, and more will be learnt about them. Hence, any initial difference between relevant and irrelevant stimuli is magnified by the inclusion of Phase 2. Again, however, this result can be explained in terms of acquired equivalence. Consider the auditory-relevant group. By the end of Phase 1 training, stimuli A and B will be associated with different responses, R1 and R2 respectively, whereas X and Y will both be associated with responses R1 and R2 equally. This arrangement should result in A and B being distinguished with ease and X and Y being treated as equivalent. Thus, assuming that 'distinctiveness' generalises to similar stimuli from the same dimension, during Phase 2, subjects will readily learn to associate C with R1 and D with R2, but will have difficulty learning about the relationship between W and Z and these responses.

Unlike the three studies mentioned thus far, the results of an IDS/EDS experiment conducted by Oswald, Yee, Rawlins, Bannerman, Good and Honey (2001) with rats cannot be explained purely in terms of an acquired equivalence account. In this experiment, three-component compounds were presented, each of which consisted of an auditory, visual and tactile element. Examples of the trial types presented during training and a subsequent test discrimination are presented in Table 3.2. In this table, tone and click represent two auditory stimuli that were presented in a testing chamber which had checked or spotted wallpaper and an uneven or smooth floor. For all subjects, the auditory and visual components were relevant during training and the tactile component was irrelevant. Thus, the tone-check and click-spot combinations were consistently reinforced, and the click-check and tone-spot combinations were consistently nonreinforced, regardless of whether they were accompanied by an uneven or smooth floor. The rats were then introduced to two

novel visual stimuli (black and white wallpaper) and two novel tactile stimuli (cool and warm floor).

Table 3.2. Examples of the Trial Types Presented During the Training and Test Discriminations for the Experiment by Oswald et al. (2001).

Training	
Tone-Check-Uneven +	Click-Check-Uneven -
Tone-Check-Smooth +	Click-Check-Smooth -
Click-Spot-Uneven +	Tone-Spot-Uneven -
Click-Spot-Smooth +	Tone-Spot-Smooth -
Test	
IDS Group	
Tone-White-Warm +	Click-White-Cool -
Tone-White-Cool +	Click-White-Warm -
Click-Black-Cool +	Tone-Black-Warm -
Click-Black-Warm +	Tone-Black-Cool -
EDS Group	
Tone-White-Warm +	Click-White-Warm -
Tone-Black-Warm +	Click-Black-Warm -
Click-White-Cool +	Tone-White-Cool -
Click-Black-Cool +	Tone-Black-Cool -

Note: Characters in bold represent elements that were relevant to the discrimination.

Half of the rats received an IDS discrimination involving these stimuli in three-component compounds, where the auditory and visual components were again relevant. Thus, the tone-white and click-black combinations were consistently reinforced, and the click-white and tone-black combinations consistently

nonreinforced, regardless of whether the floor in the testing chamber was warm or cool. The other half received an EDS discrimination, for which the auditory component was again relevant, but the visual component was irrelevant and the tactile component was now relevant. For these animals, the tone-warm and click-cool combinations were consistently reinforced, and the click-warm and tone-cool combinations were consistently nonreinforced, regardless of whether the wallpaper was black or white. The IDS group was found to acquire their test discrimination more readily than the EDS group.

The acquired equivalence account proposed by Hall (1991) is unable to account for these results. Each individual component of the compounds presented during training was reinforced on 50% of the trials on which it was presented. Thus, relevant as well as irrelevant stimuli were followed by the same outcome during training. The relevant stimuli should therefore have been treated as equivalent, and the IDS test discrimination, which was based on these stimuli, should have been acquired at an equivalent rate to the EDS discrimination. The explanation that Oswald et al. (2001) offered for their results was based on the proposal that when stimuli are presented in compound, a hidden ‘configural’ unit is formed which uniquely represents the combination of those stimuli. Similar patterns of stimulation that are followed by the same outcome (e.g. tone-check-uneven + and tone-check-smooth +) are likely to be linked to the same configural unit (say, X). Similar patterns of stimulation that are followed by different outcomes, such as tone-check-uneven + and click-check-uneven -, are likely to be linked to different configural units, say, X and Y respectively.

Stimuli which have a greater tendency to activate hidden units are assumed to be “tuned in”, and those with less tendency to activate these units are “tuned out”. The

two relevant components of the tone-check-uneven compound (tone and check) are paired with the outcome that follows them more often than the accompanying irrelevant stimulus, the uneven floor, and as a result, Oswald et al. (2001) proposed that they will become more effectively linked to the hidden unit X. It is assumed that other similar components from the relevant dimension will activate hidden units more effectively than irrelevant stimuli and other similar stimuli from the irrelevant dimension. Therefore on test, auditory and visual stimuli will be tuned in and the IDS discrimination will be acquired readily, but the EDS discrimination, for which the now relevant tactile stimuli will be tuned out, will proceed more slowly.

In summary, the majority of experiments that have investigated associability changes in rats have produced results that can be explained in terms of a non-attentional acquired equivalence account. The aim of Experiment 5 was to provide evidence to support the results of Oswald et al. (2001), which indicate that all apparent demonstrations of associability changes in rats cannot be interpreted in this way. The design of Experiment 4, which was not as complex as that used by Oswald et al., was repeated with rats in Experiment 5. Owing to the visual limitations of the rat, large black and white patterns replaced those used in Experiment 4, and rather than presenting coloured stimuli, different auditory stimuli were used.

Method

Subjects. The subjects were 32 experimentally naïve male, hooded Lister rats, which were approximately 6 months old at the start of the experiment. They were fed and maintained in the same manner as subjects in Experiments 1-3.

Apparatus and Stimuli. The same apparatus as that used in Experiment 3 was used for Experiment 5. The auditory stimuli were a 10-Hz, 70-dB clicker, a 2-kHz,



70-dB tone, a beep that consisted of 10 repetitions of a 1-s 500-Hz tone, and a whooping siren. The visual stimuli were a checkerboard pattern, a striped pattern or a spotted pattern, which always filled one of the computer screens, or the illumination of one of the screens to white. The spotted pattern consisted of a 13 x 11 matrix of black circles (diameter 1.5 cm) on a white background. The checkerboard was an 11 x 9 grid of alternating black and white squares, with each square measuring 3 x 3 cm. Finally, the striped pattern consisted of 11 alternating black and white vertical stripes, each 3 cm wide, with a height of 27 cm. For half of the animals visual stimuli appeared on the left-hand screen and for the others it appeared on the right-hand screen.

The subjects were divided into two groups; auditory-relevant and pattern-relevant, with 16 animals in each. The stimuli were counterbalanced such that for 8 subjects in each of the two groups A_1 , A_2 , A_3 and A_4 were the tone, click, beep and siren respectively, and P_1 , P_2 , P_3 and P_4 were the checkerboard, striped, spotted and white patterns respectively. For the remaining 8 animals in each group, A_1 , A_2 , A_3 and A_4 were the beep, siren, tone and click respectively, and P_1 , P_2 , P_3 and P_4 were the spotted, white, checkerboard and striped patterns respectively.

Procedure. All rats initially received 2 sessions of magazine training. During each of these 1-hr sessions, 0.2 ml of sucrose solution was delivered into the well over 3 sec, every 1 min for 30 min. The rat remained in the conditioning chamber for a further 30 min. Following magazine training, the animals were divided into two groups, auditory-relevant and pattern-relevant, with 16 animals in each. Session 1 of training began on the day following the final session of magazine training. During each of the 22 sessions of training, the two groups received each of the 16 trial types presented in Figure 3.6 twice. Each trial consisted of the

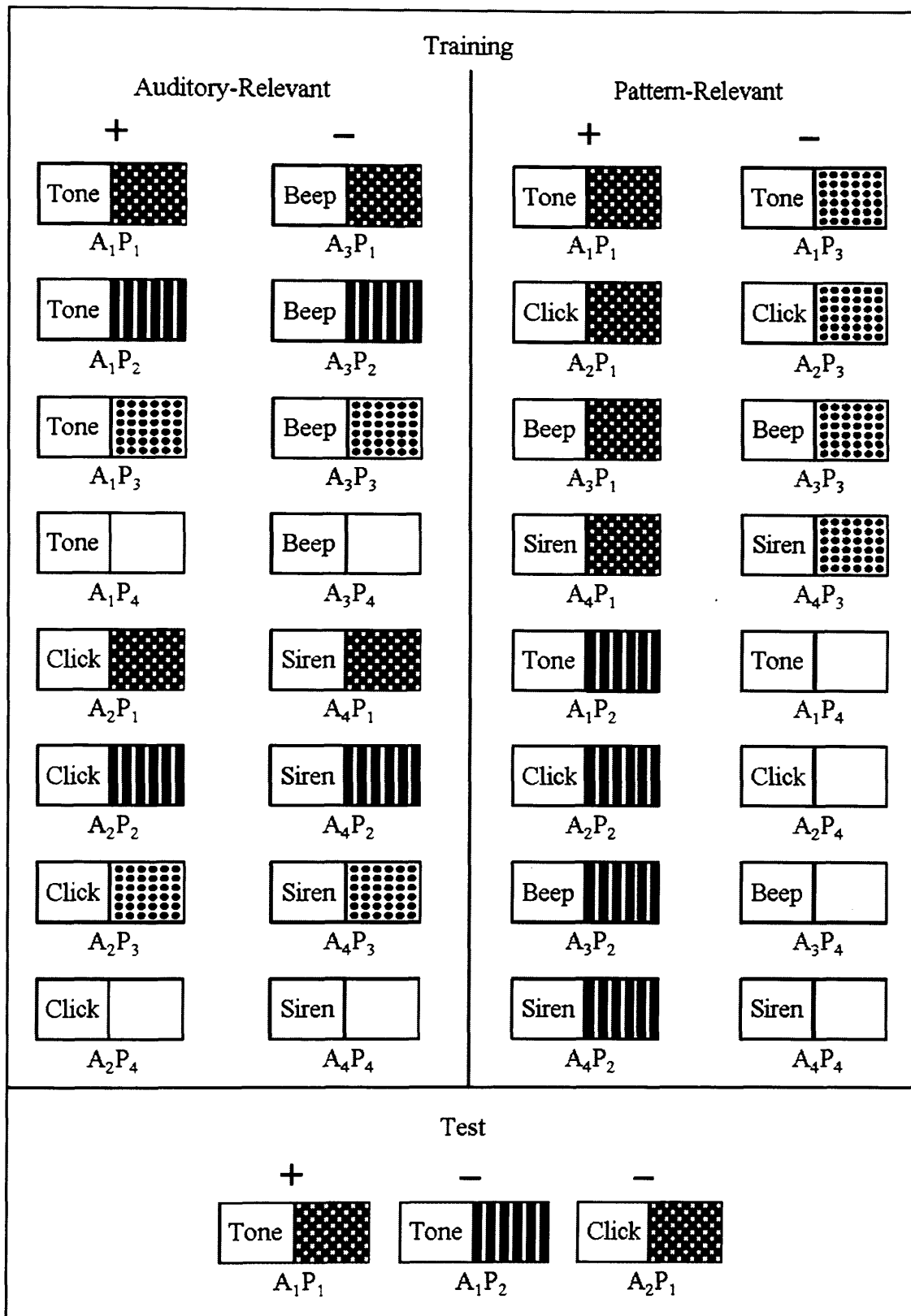


Figure 3.6. The stimuli that were used for the true discriminations and subsequent test discrimination received by the two groups in Experiment 5, for one of the counterbalanced conditions.

simultaneous presentation of an auditory stimulus from the speaker and a visual stimulus on one of the screens. For the auditory-relevant group the auditory stimuli A₁, A₂, A₃ and A₄ were relevant, with A₁ and A₂ signalling the presence of food and A₃ and A₄ signalling the absence of food. The patterns P₁, P₂, P₃ and P₄ were irrelevant. For the pattern-relevant group the patterns were relevant, with P₁ and P₂ signalling the presence of food and P₃ and P₄ signalling the absence of food. The auditory stimuli A₁, A₂, A₃ and A₄ were irrelevant.

During the 20 sessions of the test phase, all groups received the discrimination A₁P₁+ A₁P₂- A₂P₁-, which involved three compounds that had been reinforced during training (see Figure 3.6). Each session consisted of 10 presentations of the reinforced trial type, and 5 of each of the nonreinforced trial types. These three compounds were chosen in order to compare the rate at which the two groups solved a discrimination that was based on pattern stimuli (A₁P₁+ A₁P₂-), and a discrimination that was based on auditory stimuli (A₁P₁+ A₂P₁-).

The following details applied to both stages of this experiment. The intertrial interval (ITI) was randomly selected from 80 sec, 100 sec, 120 sec, 140 sec or 160 sec. For both groups, the sequence of reinforced and nonreinforced trials was random, with the constraint that no more than two trials of the same type could occur in succession. The duration spent in the magazine was recorded during each 10 sec presentation of the stimulus. Reinforcement constituted a 0.2 ml delivery of sucrose to the well over 3 sec.

Results

The mean duration of magazine activity during presentations of the eight reinforced compounds was calculated for each subject on each session of training, and

the same was done for the eight nonreinforced compounds. These data are presented for both groups in Figure 3.7.

From this figure it is evident that the auditory-relevant group acquired the discrimination between reinforced and nonreinforced trial types more readily than the pattern-relevant group. Although both groups spent similarly short durations in the magazine during nonreinforced trial types, the duration spent in the magazine during reinforced trial types increased at a slower rate in the pattern-relevant group, and had not quite reached that of the auditory-relevant group by the end of training.

A three-way analysis of variance (ANOVA) of individual mean responses during presentations of each type of CS was conducted, with the factors of group (auditory-relevant or pattern-relevant), trial type (reinforced and nonreinforced) and session, for the 22 sessions of training. The results from this ANOVA revealed a significant effect of session, $F(21, 630) = 9.24$, $MSE = 1.81$, and trial type, $F(1, 30) = 194.71$, $MSE = 8.91$, and significant Group x Trial Type, $F(1, 30) = 13.61$, $MSE = 8.91$, and Session x Trial Type $F(21, 630) = 42.40$, $MSE = 0.50$, interactions. There was no significant effect of group, $F(1, 30) = 4.05$, $MSE = 29.06$, and no Group x Session interaction, $F(21, 630) = 1.52$, $MSE = 1.81$, or Group x Session x Trial Type interaction, $F(21, 630) = 1.44$, $MSE = 0.50$. The significant interactions were analysed further using simple main effects tests, which revealed that there was an effect of trial type from Session 4 onwards, $F_s(1, 660) > 10.20$, $MSE = 0.88$, and a significant difference between the groups in the duration spent in the magazine during reinforced trial types, $F(1, 60) = 12.58$, $MSE = 18.98$.

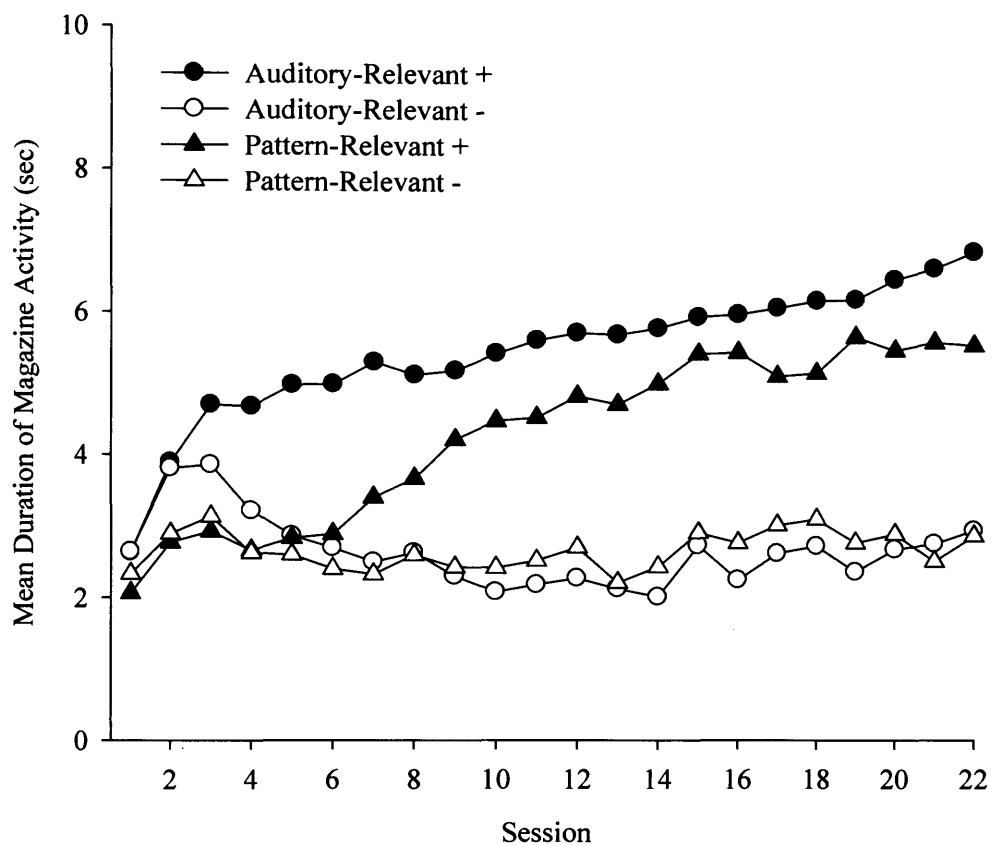


Figure 3.7. The mean rate of responding during the CS by the two groups in Experiment 5 during reinforced and nonreinforced trials of the training discrimination.

Across the 20 sessions of the test discrimination, the mean duration of magazine activity during presentations of the reinforced compound, A_1P_1 , was 6.13 s for the auditory-relevant group and 4.99 s for the pattern-relevant group. A t-test was conducted on individual mean durations of responding in the presence of this compound during the test phase, which revealed that this difference was on the borderline of statistical significance, $t(30) = 2.05$, $p = 0.05$.

There was a high level of variability in the duration spent in the magazine during presentations of the CS by the two groups. In order to minimise the influence of this variability on the interpretation of the results, discrimination ratios were calculated for every subject for each session of the test phase. These ratios were of the form $X / (X+Y)$, where X represents the mean duration of responding during presentations of the reinforced compound A_1P_1 on each session, and Y represents the mean duration of responding during presentations of one of the nonreinforced compounds (A_1P_2 or A_2P_1). A ratio of 0.5 therefore indicates a failure to discriminate between the two trial types, whereas a ratio of 1.0 indicates a perfect discrimination between them.

The mean ratio for each group for each discrimination was calculated for every session of the test phase. The data for the component of the test discrimination that was based on patterns (A_1P_1+ A_1P_2-) are presented in the upper panel of Figure 3.8. Inspection of this figure reveals that even by the end of the test phase, both groups had failed to acquire the discrimination based on patterns. A two-way ANOVA with the factors of group (auditory-relevant or visual-relevant) and session indicated that there was no effect of group, $F < 1$, session $F(19, 570) = 1.12$, $MSE = 0.01$, and no Group x Session interaction, $F(1, 30) = 1.52$, $MSE = 0.01$.

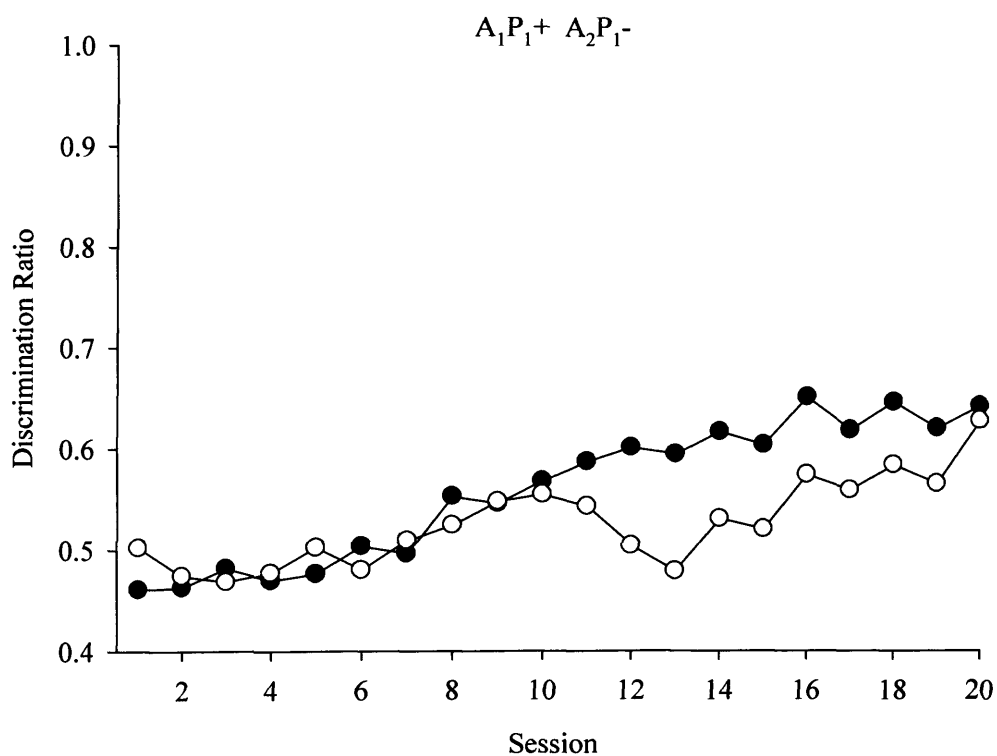
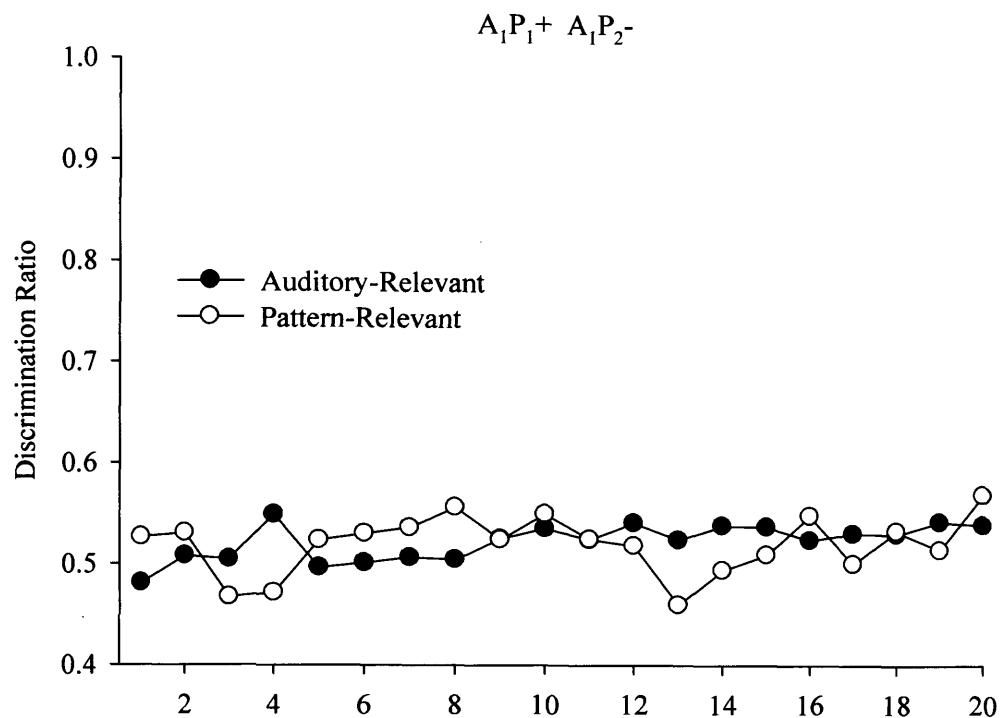


Figure 3.8. Ratios during the test stage of Experiment 5 for the discriminations based on the pattern component of the compound (upper panel) and the auditory component of the compound (lower panel).

The data for the component of the test discrimination that was based on auditory stimuli (A_1P_1+ A_2P_1-) are presented in the lower panel of Figure 3.8. From this figure, it is evident that the auditory-relevant group solved the discrimination based on two auditory stimuli that had been relevant during training more readily than subjects for whom these stimuli had been irrelevant during training. A two-way ANOVA with the factors of group (auditory-relevant or pattern-relevant) and session revealed that there was no significant effect of group, $F(1, 30) = 2.31$, $MSE = 0.08$, but that there was a significant effect of session, $F(19, 570) = 12.81$, $MSE = 0.01$, and a Group x Session interaction, $F(19, 570) = 2.33$, $MSE = 0.01$. Subsequent tests of simple main effects revealed a significant difference between the groups on Sessions 12 to 16, inclusive, $F_s(1, 600) > 4.60$, $MSE = 0.01$.

Discussion

The results of Experiment 5 demonstrate that a procedure which allows changes in attention to relevant and irrelevant stimuli to be observed in pigeons is also effective in eliciting changes in attention to certain stimuli in rats. As mentioned in the discussion to Experiment 4, these results cannot be explained in terms of acquired equivalence, an interpretation that can be applied to other demonstrations of associability changes in rats. In Experiment 5, subjects that were trained with auditory stimuli as relevant solved a subsequent test discrimination for which these stimuli were again relevant more readily than a group for which pattern stimuli had been initially relevant and auditory stimuli irrelevant. However, regardless of whether pattern stimuli had originally been trained as relevant or not, subjects failed to solve a subsequent test discrimination based on these stimuli. The slow rate at which pattern-relevant animals acquired their training discrimination indicates that subjects could

not discriminate between the patterns with ease, which could be due to their poor eyesight. Furthermore, experiments with rats rarely require subjects to discriminate as many trial types as were presented here, and the task simply could have been beyond their capabilities. Indeed, although the discriminations based on auditory stimuli were acquired more readily, by the end of the training and test phases these had only been acquired to a moderate extent.

It could be that the slightly shorter durations of magazine activity observed in the pattern-relevant group during reinforced training trials were the result of a peripheral attentional process. Holland (1977) observed that the behaviour shown by rats in the presence of visual stimuli differed from that demonstrated in the presence of auditory stimuli. Specifically, he reported that rats orient towards a visual appetitive CS for the first few seconds after its onset, and then enter the magazine, but show magazine activity throughout the presentation of an auditory CS. In the present experiment, if the pattern-relevant subjects had learned to attend preferentially to the pattern stimuli, they might be expected to show more orienting behaviours and hence less magazine activity than the auditory-relevant group. The auditory-relevant group might be expected to demonstrate more magazine activity by orienting away from the irrelevant patterns and attending preferentially to the auditory stimuli, increasing the likelihood of entering the magazine. Thus by using stimuli from two modalities but the same behavioural measurement for each, the current experiment may have failed to detect the full extent of any changes in attention.

In conclusion, although the results of Experiment 5 may not provide clear cut evidence for attentional processes during true discrimination learning in rats, they do provide a useful starting point for further investigation into these processes with rats. It could be that by using more conventional visual stimuli, such as the illumination of

different lights flashing at different rates, and exploring different response measurements, this design could prove a useful contribution to the current literature.

General Discussion

The aim of Experiments 4 and 5 was to provide evidence that associability changes occur during discrimination learning. The novel method used was particularly effective in pigeons (Experiment 4), although some evidence for similar attentional changes was also found in rats (Experiment 5). These results are inconsistent with standard associative accounts such as that proposed by Rescorla and Wagner (1972). For every subject, each compound presented in the test discrimination comprised one element that had been reinforced on 50% of its presentations during training and one element that had been previously consistently reinforced. Thus at the onset of the test discrimination the overall associative strength of each compound should have been the same. Consequently, regardless of which dimension was relevant during training, learning about the two nonreinforced compounds should have proceeded at an equal rate. The results are also inconsistent with an interpretation in terms of acquired equivalence such as that proposed by Hall (1991) to account for the IDS/EDS effect. Such an interpretation cannot explain why on test subjects readily learned about the different consequences of two stimuli that had signalled the same outcome during training.

The results can be explained by the theory of attention proposed by Mackintosh (1975a) in the following way. Mackintosh proposed that attention increases to stimuli that accurately predict the outcome that follows them. According to this theory, during training in Experiment 4, the colour-relevant group attended to colours at the expense of patterns, which then facilitated their acquisition of a subsequent

discrimination for which colours were again relevant, but hindered their acquisition of a subsequent discrimination for which patterns were relevant. The pattern-relevant group attended preferentially to patterns during training, which had the opposite effect on acquisition of the subsequent discriminations that they received.

In contrast to Mackintosh's (1975a) theory, a fundamental assumption of the Pearce-Hall (1980) model is that changes in the associability of an element within a compound are determined by the total associative strength of the compound, rather than by the associative strength of the individual element. This assumption results in the theory generating an incorrect prediction for the outcome of the test discrimination in Experiment 4. Consider the colour-relevant group, for which the colours C_1 and C_2 consistently signalled food during training, and the patterns P_1 and P_2 signalled food on just 50% of trials. On C_1P_1 trials during training, as C_1 comes to predict the outcome accurately, the Pearce-Hall model predicts that there will be a progressive decline in the associability of C_1 and P_1 . As a result, by the end of training, when C_1 fully predicts reinforcement, the associability of both C_1 and P_1 will be low. The same will be true for each of the elements within the test compounds C_1P_2 and C_2P_1 . As the associability of the previously relevant elements will be the same as that of the previously irrelevant elements from the onset of the test discrimination, there should be no difference in the rate at which subjects learn about the two nonreinforced compounds.

Having provided convincing evidence that associability changes occur during discrimination training, the mechanism that underlies these changes is of interest. Pearce et al. (2008) questioned whether this mechanism operates centrally, in accordance with the principles of Mackintosh (1975a), or peripherally. Specifically, they offered an interpretation of their results in terms of orienting responses that can

also be applied to the results of Experiment 4. In Experiment 4, the true discrimination trial types received by the colour-relevant group, for example, included: C_1P_1+ C_3P_1- , C_2P_2+ C_4P_2- . Spence (1940, p277) argued that during a visual discrimination, “the animal must learn to orient its head and eyes so as to receive the critical stimuli”. Such orienting responses are assumed to be learned as they are followed shortly afterwards by the delivery of food. Responses that provide the animal with “other sensory receptions” such as an irrelevant part of the stimulus array, are not systematically followed by food and hence tend to disappear. Therefore it could be that during training the pigeons learned to direct their gaze towards C_1 and C_2 , which were consistently followed by food, and away from the patterns that accompanied them, which were followed by reinforcement on just 50% of trials. When the test discrimination C_1P_1+ C_1P_2- C_2P_1- is presented, they would then be expected to orient towards C_1 in the compound C_1P_1 and C_2 in the compound C_2P_1 , allowing the discrimination between these two compounds to be acquired readily. However, they would also be expected to orient towards C_1 on C_1P_2 trials, and in doing so fail to learn the discrimination between this compound and C_1P_1 . This prediction was confirmed by the results of Experiment 4.

In order to test this interpretation, Pearce et al. (2008) repeated their experiment detailed in Figure 3.1, but instead of a compound stimulus comprising a plain coloured square placed next to a patterned square, each compound stimulus was a single square which contained a black pattern superimposed on a coloured background. The plain colour and pattern were integrated in this way to make it more difficult for the pigeons to look at one component of the compound and to ignore the other. Pearce et al. found that, as in their previous experiment, both a colour-relevant and pattern-relevant group learnt a subsequent discrimination that was based on

colour equally rapidly. In contrast, whereas the colour-relevant group previously had difficulty solving the test discrimination based on the patterns, when the pattern and colour were superimposed the discrimination was solved readily by both groups. This result suggests that during the previous experiment when the dimensions of colour and pattern were spatially distinct, colour-relevant animals found the test discrimination in which pattern was relevant difficult to solve as they had learnt to avert their gaze from patterns. When this strategy was prevented by integrating the two dimensions, these animals were able to solve the discrimination.

Although this explanation can account for the results of Experiment 4, the fact that associability changes were found to relevant and irrelevant auditory stimuli in Experiment 5 suggests that orienting responses are not the sole explanation for at least this result, because it is difficult to see how subjects might orient towards auditory stimuli that are relevant and away from those that are irrelevant. Further evidence that a more centrally located mechanism may underlie certain associability effects is provided by an experiment described in Chapter 1, in which Mackintosh and Little (1969) found evidence for the IDS/EDS effect when the two dimensions used were superimposed. However, as previously noted, this result has proved somewhat difficult to replicate. In light of these findings the next chapter explores further the associability changes that take place during true discrimination training and addresses the possibility that the mechanism that underlies them is located centrally rather than peripherally.

In summary, Chapter 2 provided evidence that irrelevant stimuli do not enter into the learning process. Of the theories that have been discussed in this thesis, three make this prediction: the standard associative Rescorla-Wagner (1972) model, and the theories of attention proposed by Mackintosh (1975a) and Pearce and Hall (1980). In

contrast to the assumptions of the Rescorla-Wagner model, the current chapter has provided evidence that stimuli compete for attention in order to enter the learning process, with the amount of attention they receive being determined by their relevance to the outcome that follows them. The Pearce-Hall model has been found lacking by the results of the experiments reported in this chapter, but these findings are in accordance with Mackintosh's (1975a) theory, which will be evaluated further in Chapter 4.

4. Further Analysis of the Role of Attention in Discrimination Learning

Introduction

The findings reported in the preceding chapter support the proposal that when faced with an array of stimuli, animals afford little attention to those that are irrelevant to a particular outcome, and as a result learn very little about them. Specifically, the results of Experiments 4 and 5 suggested that during the discrimination training given, attention increased to stimuli that were relevant because they were consistently followed by reinforcement. These results were interpreted in terms of the theory of attention proposed by Mackintosh (1975a). The present chapter used the novel method described in Chapter 3 to address a prediction of this theory that, to my knowledge, has never been addressed.

Mackintosh (1975a) proposed that attention increases to stimuli that are the best predictors of the outcome that follows them. It therefore follows that attention should increase not only to those stimuli that consistently signal food, but also to those that consistently signal the absence of food. Consider the compound C_3P_3 that was presented in Experiment 4 (see Figure 3.2, p74), where C_3 represented a coloured circle and P_3 represented a patterned circle. For the colour-relevant group in this experiment, C_3 consistently signalled nonreinforcement, and was thus a better predictor of this outcome than P_3 , which was followed by food on 50% of its presentations. According to Mackintosh, the direction of change in the associability of C_3 on a C_3P_3 trial is determined by Equations 4.1 and 4.2. As C_3 is a more accurate predictor of the outcome than P_3 on these trials, the discrepancy $\lambda - V_{C_3}$ will be smaller than the discrepancy $\lambda - V_{P_3}$, leading to an increase in the associability of C_3 .

Similarly, P_3 will suffer a decline in associability as it is a less accurate predictor than C_3 , the stimulus that accompanies it.

$$\Delta\alpha_{C3} \text{ is positive if } |\lambda - V_{C3}| < |\lambda - V_{P3}| \quad (4.1)$$

$$\Delta\alpha_{C3} \text{ is negative if } |\lambda - V_{C3}| \geq |\lambda - V_{P3}| \quad (4.2)$$

Changes in the associative strength of C_3 are determined by its associability multiplied by the discrepancy $\lambda - V_{C3}$ (see Equation 4.3). Thus the high associability of C_3 established during training should facilitate subsequent learning about this stimulus.

$$\Delta V_{C3} = \alpha_{C3}\theta (\lambda - V_{C3}) \quad (4.3)$$

In Chapter 3 it was argued that the attentional changes observed in Experiment 4 in particular could be explained if it is assumed that attention was driven by orienting responses rather than according to Mackintosh's (1975a) principles. Specifically, it was argued that during training subjects might have learned to orient towards features that were consistently reinforced, as these stimuli were presented in close contiguity with food, and to avert their gaze from the irrelevant accompanying stimuli because they were not followed by food as frequently. The implication of this analysis for Experiment 4 is that subjects will fail to orient towards both irrelevant features and relevant features that are consistently followed by nonreinforcement. Indeed Hearst and Franklin (1977) provided some evidence in support of this claim, demonstrating that pigeons actively withdraw from stimuli that are consistently followed by the absence of food. Thus according to the account based on orienting

responses, both irrelevant stimuli and relevant stimuli that are consistently followed by nonreinforcement will receive little attention. In fact, more attention might be paid to irrelevant stimuli, which are intermittently paired with food, than to those relevant stimuli that are never paired with food. In contrast, Mackintosh assumes that irrelevant stimuli will be treated very differently from relevant stimuli that consistently signal nonreinforcement, with the former receiving very little attention, and the latter receiving considerable attention.

Experiment 6 was designed to evaluate these two accounts, with the aim of investigating further the mechanism underlying the changes in attention observed in the preceding chapter. The design of this experiment is presented in Figure 4.1. The training given was identical to that in Experiment 4. Thus for a colour-relevant group of pigeons, presentations of the colours C_1 and C_2 were consistently followed by food, and C_3 and C_4 were consistently followed by the absence of food. The patterns P_1 , P_2 , P_3 and P_4 were irrelevant, with each being followed by food on 50% of presentations. For a pattern-relevant group, the patterns P_1 and P_2 were consistently followed by food, and P_3 and P_4 consistently followed by the absence of food. The colours C_1 , C_2 , C_3 and C_4 were irrelevant to the outcome that followed them.

Of interest was the associability of stimuli that had previously signalled the absence of food, and thus three compounds that had been nonreinforced during training were used in the test stage. It might be expected that compounds that had been nonreinforced during training would simply not elicit any responding when presented on test. However, previous experiments conducted in our laboratory that have used autoshaping have revealed that when presented with an unfamiliar discrimination, pigeons soon start pecking at a high rate to all stimuli involved. By presenting Test 1 detailed in Figure 4.1, subjects were expected to respond at a









































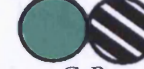
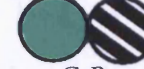












Training					
Colour-Relevant			Pattern-Relevant		
+		-	+		-
					
C_1P_1	C_3P_1	C_1P_3	C_1P_1	C_1P_3	C_1P_4
					
C_1P_2	C_3P_2	C_3P_3	C_2P_1	C_2P_3	C_2P_4
					
C_1P_3	C_3P_3	C_3P_4	C_3P_1	C_3P_3	C_3P_4
					
C_1P_4	C_3P_4	C_4P_1	C_4P_1	C_4P_3	C_4P_4
					
C_2P_1	C_4P_1	C_4P_2	C_1P_2	C_1P_4	C_1P_3
					
C_2P_2	C_4P_2	C_4P_3	C_2P_2	C_2P_4	C_2P_1
					
C_2P_3	C_4P_3	C_4P_4	C_3P_2	C_3P_4	C_3P_1
					
C_2P_4	C_4P_4		C_4P_2	C_4P_4	
Test 1		+	-	-	
					
	C_3P_3	C_3P_4	C_4P_3		
Test 2					
					
	C_1P_1	C_1P_2	C_2P_1		

Figure 4.1. The stimuli that were used for the true discriminations and subsequent test discriminations received by the two groups in Experiment 6, for one of the counterbalanced conditions. After the completion of training, all subjects received 10 sessions of Test 1 followed by 10 sessions of Test 2.

relatively high level to all three compounds in the early stages of the test phase, and gradually stop responding to C_3P_4 and C_4P_3 as they began to learn the discrimination.

As in Experiment 4, Test 1 involved a discrimination based on stimuli that had been relevant during training, and a discrimination based on stimuli that had been irrelevant during training. The discrimination C_3P_3+ C_4P_3- was based on two colours, C_3 and C_4 , that had been consistently nonreinforced for the colour-relevant group during training. The prediction derived from the theory proposed by Mackintosh (1975a) was that attention should have increased to C_3 and C_4 during training in this group because these stimuli were better predictors of the absence of food than the pattern stimuli that accompanied them. Thus on test, this group would be expected to acquire the C_3P_3+ C_4P_3- discrimination more readily than the pattern-relevant group, for which the colours C_3 and C_4 were irrelevant during training. The discrimination C_3P_3+ C_3P_4- was based on two patterns, P_3 and P_4 , that were consistently nonreinforced during training in the pattern-relevant group. Thus in this group attention should have increased to these stimuli during training, at the expense of the colours that accompanied them. This group should therefore acquire the discrimination C_3P_3+ C_3P_4- more readily than the colour-relevant group, for which P_3 and P_4 were poor predictors of the outcome during training.

According to the orienting responses account, the colour-relevant group, for example, should have learned to avert their gaze from features C_3 and C_4 which were consistently nonreinforced during training. Thus when presented with the test discrimination C_3P_3+ C_4P_3- , for which C_3 and C_4 were again relevant, they would be expected to orient away from these features and in doing so fail to acquire the discrimination. In this case, the discrimination C_3P_3+ C_3P_4- , which is based on patterns might be solved more readily, as subjects would be expected to divert their

gaze away from the colours and perhaps towards the previously irrelevant patterns. A similar reversal of Mackintosh's (1975a) predictions would be expected for the pattern-relevant group.

A second test discrimination, identical to that presented in the test phase of Experiment 4, was given following Test 1. This discrimination involved presenting three compounds that had been consistently reinforced for both groups during training, and was conducted to confirm the reliability of the results reported in Chapter 3. Again, it was predicted that the colour-relevant group would acquire a discrimination based on colours that had been consistently reinforced in this group during training more readily than the pattern-relevant group, and vice versa for a discrimination based on patterns that had been consistently reinforced for the pattern-relevant group during training.

Experiment 6

Method

Subjects. The subjects were 16 experimentally naïve adult homing pigeons. They were fed and maintained in the same manner as subjects in Experiment 4.

Apparatus and Stimuli. The stimuli and apparatus were the same as those used in Experiment 4. The stimuli were counterbalanced in the same way, such that for half of the subjects C₁, C₂, C₃, and C₄ represented cyan, yellow, green and magenta respectively, and P₁, P₂, P₃, and P₄ represented lines of orientation 0°, 90°, 45°, and -45° respectively. For the other half, C₁, C₂, C₃, and C₄ represented yellow, cyan, magenta and green respectively, and P₁, P₂, P₃, and P₄ represented lines of orientation 90°, 0°, -45° and 45° respectively.

Procedure. Eight animals were assigned to the colour-relevant group, and eight to the pattern-relevant group. Magazine training and autoshaping proceeded in the same manner as in Experiment 4. Session 1 of training began on the day after the final session of autoshaping. There were 64 trials in each of the 20 sessions of training. Each of the trial types presented in Figure 4.1 was presented twice with the coloured circle on the left, and twice with the coloured circle on the right. During the 10 sessions of Test 1, subjects received three trial types that had been nonreinforced during training; C_3P_3 , C_3P_4 and C_4P_3 . C_3P_3 was presented 20 times in each session, and was always reinforced. C_3P_4 and C_4P_3 were each presented 10 times, and remained nonreinforced. During Test 2, presentations of three trial types that had been reinforced during training were presented; C_1P_1 , C_1P_2 and C_2P_1 . The 20 presentations of C_1P_1 in each session were reinforced, whilst the 10 presentations of each of the other compounds were nonreinforced. All other procedural details for this experiment were the same as for Experiment 4.

Results

The mean rate of responding during presentations of the eight reinforced compounds was calculated for each subject for every session of training and the same was done for the eight nonreinforced compounds. The data for both groups are presented in Figure 4.2. Inspection of this figure suggests that, as in Experiment 4, the colour-relevant group acquired the discrimination between reinforced and nonreinforced trial types more readily than the pattern-relevant group, but by the end of training both groups were responding at a comparably high rate during reinforced trial types and a similarly low rate during nonreinforced trial types.

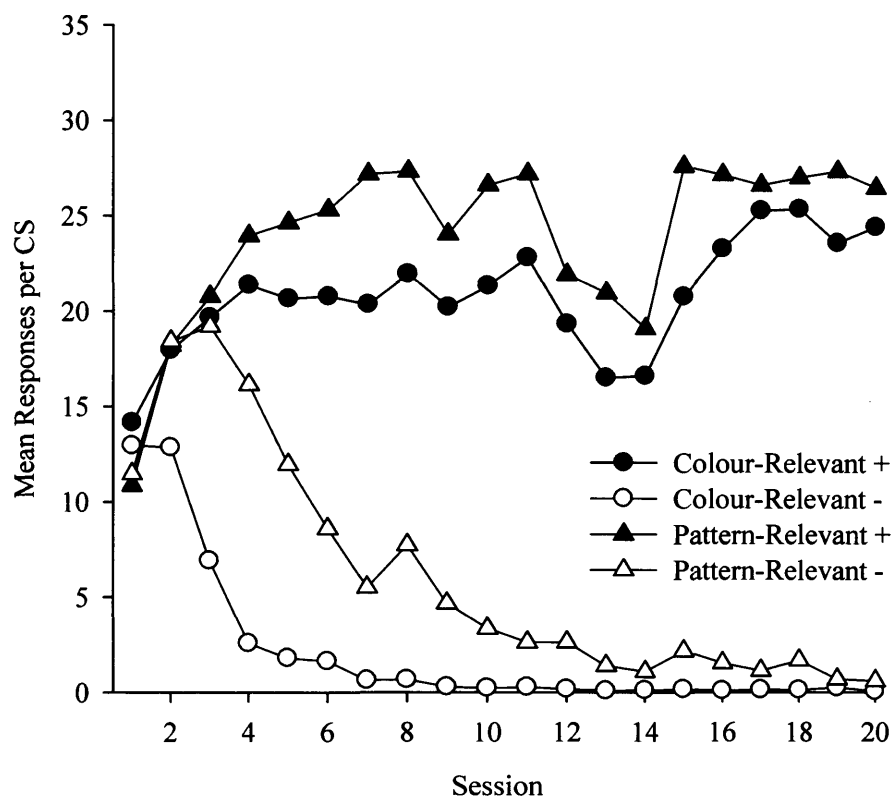


Figure 4.2. The mean rate of responding during the CS by the two groups in Experiment 6 during reinforced and nonreinforced trials of the training discrimination.

A three-way analysis of variance (ANOVA) of individual mean responses during presentations of each trial type was conducted, with the factors of group (colour-relevant or pattern-relevant), trial type (reinforced and nonreinforced) and session, for the 20 sessions of training. The results from this ANOVA revealed a significant effect of session, $F(19, 266) = 4.00$, $MSE = 30.18$, trial type, $F(1, 14) = 147.90$, $MSE = 365.63$, and group, $F(1, 14) = 6.39$, $MSE = 329.06$, and significant Group x Session, $F(19, 266) = 1.67$, $MSE = 30.18$, Trial Type x Session, $F(19, 266) = 21.63$, $MSE = 20.43$, and Group x Trial Type x Session, $F(19, 266) = 1.95$, $MSE = 20.43$, interactions. The Group x Trial Type interaction was not significant, $F < 1$. The three-way interaction was analysed using simple main effects tests, which confirmed that the two groups acquired the discrimination at different rates; there was a significant difference between responding during the two trial types from Session 3 onwards in the colour-relevant group, $F_s(1, 280) > 17.28$, $MSE = 37.69$, and from Session 4 onwards in the pattern-relevant group, $F_s(1, 280) > 6.50$, $MSE = 37.69$. The Group x Session interaction was only significant for nonreinforced trials, $F(19, 532) = 2.68$, $MSE = 25.31$, and simple main effects tests revealed that responding during these trials was significantly different in the two groups on Sessions 3, 4, 5, 6 and 8, $F_s(1, 560) > 4.69$, $MSE = 41.41$.

Inspection of response rates during Test 1 revealed a rather complex pattern of results. For this reason, discrimination ratios were not considered to provide a clear representation of the data. The mean rate of responding during presentations of the reinforced compound, C₃P₃, on each session is shown for the two groups in the left-hand panel of Figure 4.3. Responding in the presence of this compound began at a low level which increased throughout Test 1 at a comparable rate in the colour-relevant and pattern-relevant groups. A two-way ANOVA of individual mean number of

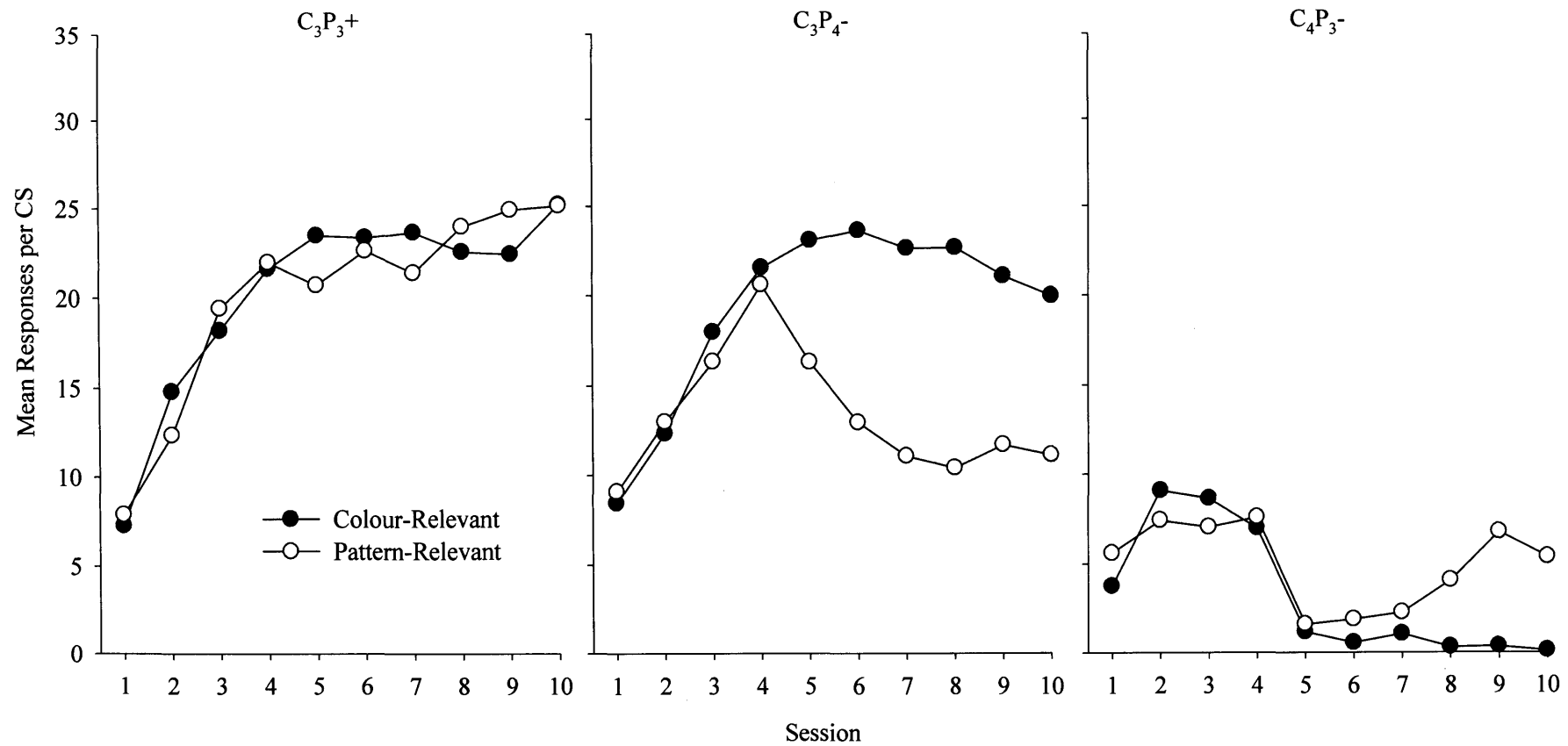


Figure 4.3. The mean rate of responding during the CS for the two groups on each session of Test 1 of Experiment 6, for the reinforced compound C_3P_3 (left-hand panel), the compound C_3P_4 where the distinctive cue was the pattern (centre panel) and the compound C_4P_3 where the distinctive cue was the colour (right-hand panel).

responses made in the presence of this compound was conducted, with the factors of group (colour-relevant or pattern-relevant) and session. This analysis revealed a significant effect of session, $F(9, 126) = 16.21$, $MSE = 29.33$, but no effect of group or Group x Session interaction, $F_s < 1$.

The mean number of responses made during presentations of C_3P_4 , where the distinctive feature is the pattern, is shown for each session of Test 1 for the two groups in the centre panel of Figure 4.3. Inspection of this figure reveals that both groups failed to discriminate between C_3P_3+ and C_3P_4- for the first four sessions of Test 1, which presumably reflects the low salience of patterns relative to colours. After Session 4, responding in the presence of this compound extinguished rapidly in the pattern-relevant group, but remained at a high level in the colour-relevant group. A two-way ANOVA of individual mean number of responses made in the presence of this compound was conducted, with the factors of group (colour-relevant or pattern-relevant) and session. This analysis revealed a significant effect of session, $F(9, 126) = 5.95$, $MSE = 32.84$. The effect of group failed to reach significance, $F(1, 14) = 3.63$, $MSE = 408.84$, but the Group x Session interaction was significant, $F(9, 126) = 3.32$, $MSE = 32.84$. Simple main effects tests used to analyse this interaction revealed that there was an effect of group on Sessions 6, 7, 8, 9 and 10, $F_s(1, 140) > 4.47$, $MSE = 70.44$.

The mean number of responses made during presentations of C_4P_3 on each session is shown for the two groups in the right-hand panel of Figure 4.3. From the onset of Test 1, both groups responded at a minimal level in the presence of this compound, for which colour was the distinctive feature. This finding can again be explained by the salience of colours being higher than that of patterns. An apparent difference began to emerge between the two groups from Session 5, when responding resumed in the pattern-relevant group. A two-way ANOVA of individual mean number of responses made in the

presence of C_4P_3 , with the factors of group (colour-relevant or pattern-relevant) and session was conducted. This analysis revealed a significant effect of session, $F(9, 126) = 3.95$, $MSE = 31.09$, but no effect of group, $F(1, 14) = 1.03$, $MSE = 120.37$, and no significant Group x Session interaction $F < 1$. Out of interest, simple main effects tests were conducted to investigate the apparent difference between the two groups in the latter half of the test phase. These tests revealed that this difference was only significant on Session 9, $F(1, 140) = 4.13$, $MSE = 40.02$.

The mean response rate during presentations of the reinforced compound C_1P_1 across the 10 sessions of Test 2 combined was 21.21 for the colour-relevant group, and 24.67 for the pattern-relevant group. A two-way ANOVA of individual mean number of responses made in the presence of C_1P_1 , with the factors of group (colour-relevant or pattern-relevant) and session, revealed that there was no significant effect of session, $F(9, 126) = 1.28$, $MSE = 17.53$, or group, $F < 1$, and no Group x Session interaction, $F < 1$.

For Test 2, discrimination ratios were calculated for each subject on every session for the component of the discrimination where patterns were relevant (C_1P_1+ C_1P_2-) and the component of the discrimination where colours were relevant (C_1P_1+ C_2P_1-). The mean discrimination ratios for the two groups are presented in Figure 4.4. Inspection of the upper panel of Figure 4.4 suggests that the pattern-relevant group acquired the discrimination for which patterns were relevant more rapidly than the colour-relevant group, which had not acquired this discrimination by the end of training. A two-way ANOVA was conducted on individual mean discrimination ratios during each session of the test phase with the factors of group (colour-relevant or pattern-relevant) and session. This analysis revealed that there was a significant effect of group, $F(1, 14) = 12.00$, $MSE = 0.06$, and session, $F(9, 126) = 5.40$, $MSE = 0.02$, and no significant Group x Session interaction, $F(9, 126) = 1.65$, $MSE = 0.02$.

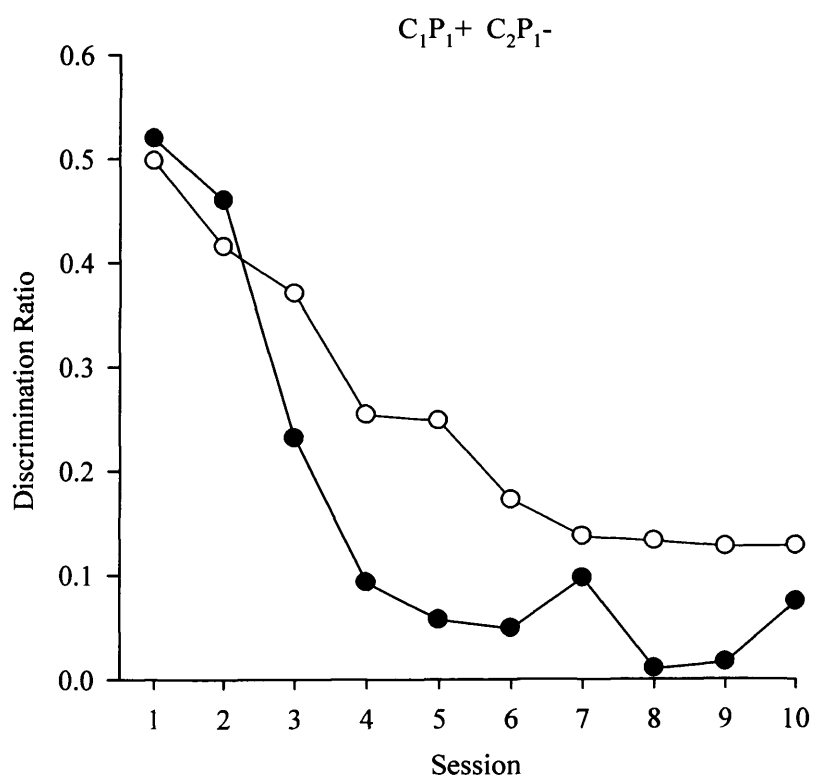
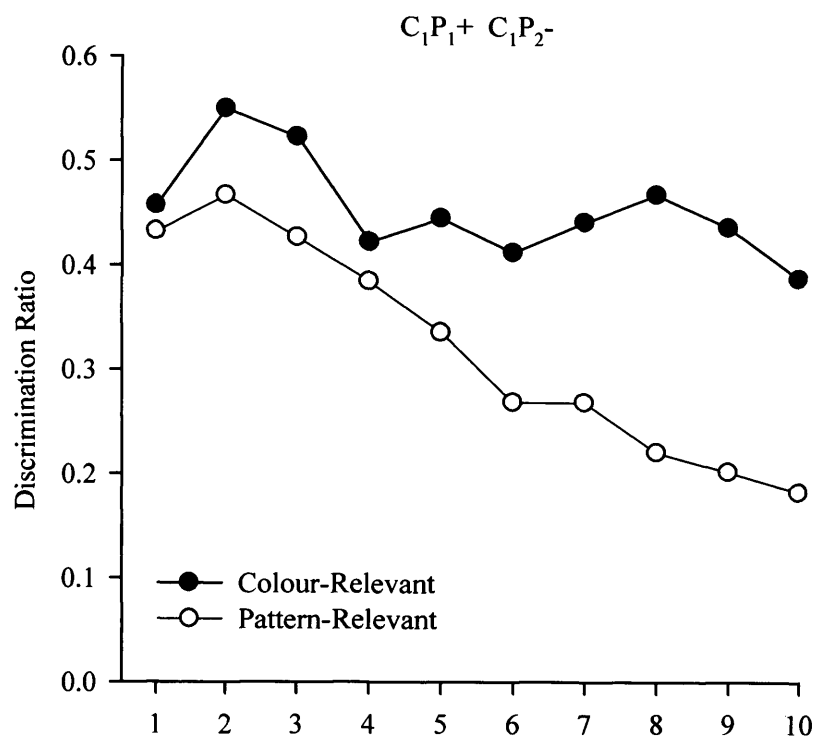


Figure 4.4. Mean discrimination ratios for the two groups for each session of Test 2 during Experiment 6, for the discrimination where patterns were relevant (upper panel) and the discrimination where colours were relevant (lower panel).

Inspection of the lower panel of Figure 4.4 suggests that the colour-relevant group acquired the discrimination for which colours were relevant more rapidly than the pattern-relevant group. This observation was confirmed by a two-way ANOVA conducted on individual mean discrimination ratios during each session of the test phase with the factors of group (colour-relevant or pattern-relevant) and session. This analysis revealed that there was no significant effect of group, $F(1, 14) = 3.59$, $MSE = 0.09$, but there was a significant effect of Session, $F(9, 126) = 52.88$, $MSE = 0.01$, and a significant Group x Session interaction, $F(9, 126) = 3.28$, $MSE = 0.01$. This interaction was analysed using simple main effects tests, which confirmed that there was a significant effect of group on Sessions 3, 4, 5 and 6, $F_s(1, 140) > 3.99$, $MSE = 0.02$.

Discussion

In support of the results of Experiment 4, Test 2 given in Experiment 6 provided evidence that attention increases to stimuli that are relevant during discrimination learning because they consistently signal reinforcement. The results of Test 1 extended these findings by suggesting that comparable changes in attention affect stimuli that are relevant because they consistently signal nonreinforcement, a prediction derived from the theory of attention proposed by Mackintosh (1975a) that has never been tested.

During Test 1, subjects received the discrimination C_3P_3+ C_3P_4- C_4P_3- . The results of this test demonstrated convincingly that the pattern-relevant group solved the discrimination based on patterns that had previously been consistently nonreinforced (C_3P_3+ C_3P_4-) more rapidly than the colour-relevant group, for which these patterns had been previously irrelevant. The results for the discrimination based on colours (C_3P_3+ C_4P_3-) were less clear cut. Both groups responded at a very low level in the presence of C_4P_3- from the outset of Test 1, but responding to this trial type began to increase in the

pattern-relevant group midway through the test phase. During the initial sessions of Test 1, responding to the compound $C_3P_4^-$, where the distinctive cue was the pattern, increased in both groups. It could be that the decrease in responding to this compound observed in the pattern-relevant group from Session 5 reflects the fact that this group is beginning to pay attention to patterns. If this were the case, then the pattern P_3 would also be expected to gain attention in the pattern-relevant group. As a result of this increase in attention, P_3 would gain associative strength when it is reinforced in compound with C_3 , which could cause the increase in responding to the compound C_4P_3 that is observed in the pattern-relevant group.

Test 2 was conducted in an attempt to replicate the results of Test 1 reported in Experiment 4. The results of this test demonstrated that a discrimination based on patterns was acquired more readily by a group for which these features had been consistently reinforced during training than a group for which these features had previously been irrelevant. A similar observation was made for the discrimination based on colours. Despite supporting the interpretation of the results of Experiment 4, the results of Test 2 should be interpreted with a degree of caution, as these findings may not have been the result of changes in attention established during training, but of changes in attention during Test 1.

During Test 1, after a few sessions the pattern-relevant group showed rapid extinction to the compound where the distinctive cue was the pattern (C_3P_4), implying that attending to patterns during training had facilitated their learning of the discrimination between this compound and $C_3P_3^+$. The discrimination based on patterns during Test 2 ($C_1P_1^+ - C_1P_2^-$) was acquired readily by the pattern-relevant group, but whether learning about this compound was facilitated by an increase in attention to patterns established during training or during Test 1 is unclear. It was suggested earlier

that when learning the discrimination that was based on colours in Test 1 (C_3P_3+ C_4P_3-), rather than learning to attend to the colours, after a few sessions the pattern-relevant group began attending to the pattern P_3 . Such an interpretation could explain why this group had difficulty acquiring a subsequent discrimination based on colours in Test 2. Similarly, responding to the compound C_3P_4- in the colour-relevant group appears to have decreased slightly by the end of Test 1, suggesting that this group may have begun to pay some attention towards patterns. This group went on to acquire the subsequent discrimination based on patterns with considerably more ease, suggesting that the discrimination based on patterns given in Test 1 may have facilitated their learning the discrimination based on patterns given in Test 2.

The results of Test 2 are, however, not the primary source of interest. The critical data of Experiment 6 are those from Test 1, which provide evidence that during training attention increased to stimuli that consistently signalled nonreinforcement. Research has suggested (e.g. Hearst and Franklin, 1977) that animals withdraw from stimuli that signal nonreinforcement. If similar orienting responses played a key role in Experiment 6 the colour-relevant group, for example, would have oriented away from C_3 and C_4 during training, because these colours were consistently followed by the absence of food. The colour-relevant group would then be expected to orient away from these features when they were presented again on test. As a result, the component of the discrimination presented in Test 1 that was based on these features (C_3P_3+ C_4P_3-) should be difficult for this group. In contrast, acquisition of the discrimination between C_3P_3+ C_3P_4- might be expected to proceed more readily, as subjects would avert their gaze from C_3 , increasing the likelihood of paying attention to P_3 and P_4 , the relevant features for this discrimination. In fact, the opposite pattern of results was observed.

The question remains why, using a similar design and stimuli, Pearce et al. (2008) found that a peripheral orienting process seemed to be responsible for the changes in attention that they observed. It could be that the method they used for assessing the involvement of orienting responses was simply not appropriate. As described in Chapter 3, their experiment involved integrating colours and patterns that had, in a previous experiment, appeared in distinct spatial locations. Integrating colour and pattern in this way could have prevented the pigeons from differentiating the two dimensions and learning that one was relevant to the delivery of reinforcement and the other was irrelevant. Instead, subjects might simply have learned whether each particular combination of colour and pattern presented led to reinforcement or nonreinforcement (e.g. Pearce, 1994). This explanation would account for the observation that during the subsequent test discrimination, two trial types that had previously signalled reinforcement were learned about at the same rate, regardless of whether their distinctive feature had been relevant or irrelevant during training.

It may be that orienting responses were involved in Experiment 6, but operate in a different manner to that previously discussed. It has been assumed thus far that if an orienting response is directed towards a feature that is consistently followed by reinforcement, that response is reinforced because it occurs in close contiguity with food. Orienting towards a feature that is consistently followed by the absence of food will not be reinforced in the same way and so will disappear. Wyckoff (1952) used the term 'observing response' to refer to any response which results in exposure to the stimuli that are to be discriminated. This term therefore encapsulates the orienting response discussed above. It also refers to a response, such as a lever press, which results in the presentation of the stimuli to be discriminated.

This latter observing response was studied by Lieberman (1972), who questioned whether such responses were made because they were associated with reinforcement, or because they reduced uncertainty. Monkeys were trained to press a lever for food. In the presence of a tone, one in 50 responses was rewarded on a variable ratio schedule (VR), and in the presence of a light no reward was ever given (extinction). Following this stage, another lever was inserted into the testing chamber. The tone and light cues were no longer presented, but pressing the new lever produced a 6-sec presentation of one of these cues, indicating which reinforcement schedule was in effect. Pressing this lever therefore constituted an observing response. The same training continued, but after each press of the food lever on the VR schedule, a brief flash of light was presented. Food lever presses on the extinction schedule were followed by nothing. During this stage, the light flashes provided information about the reinforcement schedule that was in effect, and subjects made few observing responses. In a final stage, training proceeded without the flashes of light following responses on the food lever, and an increase in observing responses was recorded. Whether the light flashes were present or not, the observing response was followed by the same reinforcement schedule, therefore this change in the observing response could not be interpreted in terms of its association with reinforcement. Instead, Lieberman (1972) concluded that it was caused by the increase in uncertainty produced by the removal of the flashing light.

In a further experiment, the same procedure was used with the exception that in the final stage, the light flashes continued to follow lever presses made on the VR schedule, but making the observing response during the extinction schedule did not produce the appropriate 6-sec cue. Lieberman (1972) reported that observing responses were initially high when the extinction schedule was in effect, but when this response no longer produced the informative cue, it was not made. Thus, a stimulus that was

consistently followed by nonreinforcement reinforced the observing response, such that when this stimulus was no longer presented, the observing response extinguished.

The fact that a stimulus which was never presented in close contiguity with food can reinforce observing behaviour suggests that in the current experiment, a feature that was consistently followed by the absence of food could still reinforce an orienting response towards it by virtue of it being an informative stimulus. However, it should be noted that this effect has not been replicated in pigeons. Mueller and Dinsmoor (1984) used a method very similar to that used by Lieberman (1972), in which pigeons were required to press a pedal in order to gain information about the reinforcement schedule currently in effect. They found that when the observing response did not produce the stimulus signalling a VR schedule, but did produce the stimulus signalling the extinction schedule, the observing response declined reliably. That is, the CS- alone did not maintain the observing response. It was therefore concluded that the results should not be attributed to the fact that the stimulus signalling nonreinforcement was reinforcing. Blanchard (1975) also reported evidence that rather than having a reinforcing effect on observing behaviour in pigeons, presentations of CS- had a punishing effect.

Thus an explanation for the results of Experiment 6 in terms of orienting responses may not be feasible. Instead, these results appear to be explained better by an attentional mechanism such as that proposed by Mackintosh (1975a), which operates once stimuli have been perceived. Although I know of no other experiment with pigeons that has tested the assumption that attention increases to stimuli that consistently signal nonreinforcement, an experiment conducted by Whitney and White (1993), for which the subjects were humans, appears to provide some support for this prediction. In their experiment, the length of a line presented to subjects was relevant to a discrimination, and the orientation of that line was irrelevant. Subjects were required to respond 'yes' to lines

that were 20 mm in length, and ‘no’ to lines that were 8 mm in length. One IDS group was then presented with a transfer discrimination during which they were required to respond ‘yes’ to 18-mm lines. An IDS-reversal group was required to respond ‘yes’ to 8-mm lines. Despite the fact that lines similar to this length had initially been incorrect (analogous to being nonreinforced), this group acquired the transfer discrimination as readily as the standard IDS group. This result can be explained if it is assumed that attention increased to the individual stimuli presented during the original discrimination, which facilitated subsequent learning about them regardless of whether they had initially been correct or incorrect (reinforced or nonreinforced).

In summary, Experiment 6 provided further evidence that changes in attention occur during simple discrimination learning, and produced the novel finding that these changes occur to stimuli that are relevant because they consistently signal the absence of food. This result is difficult to explain by appealing to orienting responses, but is consistent with the principles of the theory of attention proposed by Mackintosh (1975a). Thus rather than involving a peripheral process that directs gaze, enabling subjects to perceive certain stimuli at the expense of others, it is suggested that a central mechanism which operates once these stimuli have been perceived is involved in learning of this kind. Experiment 7 reported in the next chapter was designed to test further this interpretation of the results.

5. Further Analysis of the Theory of Attention Proposed by Mackintosh (1975a)

Introduction

The experiments reported thus far have suggested that there is a need to incorporate an attentional mechanism into any theory of learning that is to successfully explain the fate of irrelevant stimuli during discrimination learning. However, before concluding that such a mechanism is indeed necessary to explain the preceding results, a final attempt will be made to rule out other accounts.

Numerous experiments (e.g. Mackintosh, 1974) have shown that behaviour that has been reinforced intermittently extinguishes more slowly than behaviour that has been reinforced consistently. This finding is referred to as the partial reinforcement extinction effect. An autoshaping experiment with pigeons reported by Rescorla (1999) demonstrates the relevance of this effect to the experiments reported here. In Rescorla's experiment subjects received presentations of stimulus A that were consistently reinforced, and presentations of stimulus B that were reinforced 50% of the time. When these two stimuli were subsequently presented in extinction, subjects were slower to stop responding to B than to A. Consider the test discrimination presented in Experiment 4 which involved the compounds C_1P_1+ C_1P_2- and C_2P_1- . During this discrimination, the elements P_2 and C_2 were the distinctive features of the compounds C_1P_2 and C_2P_1 respectively. The colour C_2 was consistently reinforced in the colour-relevant group during training, and partially reinforced in the pattern-relevant group. Thus the colour-relevant group would be expected to stop responding to C_2P_1 more quickly than the pattern-relevant group, and in doing so acquire the discrimination C_1P_1+ C_2P_1- more readily. The pattern P_2 was consistently reinforced in the pattern-relevant group during training, and partially reinforced in the colour-relevant group. Thus in this case the

pattern-relevant group would be expected to stop responding to C_1P_2 more quickly than the colour-relevant group, and in doing so acquire the discrimination C_1P_1+ C_1P_2- more readily. These were precisely the effects observed in Experiment 4.

A non-attentional mechanism proposed by Rescorla (2001) also has the potential to explain the results of Experiment 4. Rescorla's experiments involved an autoshaping procedure with pigeons, the basic design of which is presented in Table 5.1. Initially subjects received extensive pre-exposure with the stimuli A, B, C and D, which were lines of different colours, before conditioning with two of these stimuli, A and C. In one experiment, a compound consisting of A and B was then reinforced; in another, presentations of this compound were nonreinforced. Finally, subjects received a test of the compounds AD and BC.

Table 5.1. Basic Design of Experiments 3 and 4 from Rescorla (2001).

Pre-exposure				Conditioning		Compound Training	Test	
A-	C-	B-	D-	A+	C+	AB+ or AB-	AD-	BC-

Rescorla (2001) observed greater responding to BC than to AD both when presentations of AB were reinforced and when presentations of AB were nonreinforced. Thus the associative strength of the BC compound was greater than that of the AD compound in both experiments. The implication of this result is that reinforcement of AB produced a greater increment in the associative strength of neutral B than it did in the associative strength of excitatory A, and that nonreinforcement of AB produced a greater decrement in the associative strength of the excitatory A than the neutral B. Rescorla suggested that these findings could be explained if it is assumed that the error term within the Rescorla-Wagner (1972) model was modulated by the distance of each element in the compound from asymptote, such that learning proceeds faster to stimuli that are further

from the asymptote. Applied to the experiments described in Table 5.1, when AB is reinforced during compound training, A already has high associative strength and is therefore close to the asymptote of a reinforced trial. The associative strength of B is close to the asymptote of a nonreinforced trial, zero, and hence is further away from asymptote during AB+ training than A. According to Rescorla, B will gain associative strength more quickly than A during compound conditioning. Thus on test, the overall associative strength of the BC compound will be higher than that of the AD compound, and BC will elicit more responding than AD. When AB is nonreinforced, A is further away from the asymptote of zero on AB- trials than B is, meaning that A will lose associative strength more quickly than B, and again more responding is expected to BC than to AD.

This explanation can be applied to Experiment 4 in the following way. From the onset of the test discrimination C_1P_1+ C_1P_2- C_2P_1- , the associative strength of C_2 is higher in the colour-relevant group, for which it was consistently reinforced during training, than in the pattern-relevant group, for which it was partially reinforced. The difference between C_2 and the asymptote of the C_2P_1- trial (zero) will therefore be greater in the colour-relevant group than in the pattern-relevant group, with the result that learning about the outcome of this trial type, and hence the discrimination C_1P_1+ C_2P_1- , will proceed more quickly in the former group than in the latter. A similar explanation can be applied to responding to C_1P_2 , where as a result of training the distinctive element in this compound (P_2) has higher associative strength and is therefore further away from asymptote in the pattern-relevant group than in the colour-relevant group. The C_1P_1+ C_1P_2- discrimination should therefore be acquired more rapidly by the pattern-relevant group than the colour-relevant group.

At first sight, it seems that the preceding interpretation of Rescorla's (2001) account cannot explain the results of Test 1 from Experiment 6. Here, the test discrimination involved compounds that had been consistently nonreinforced during training: C_3P_3+ C_3P_4- C_4P_3- . Consider, for example, the compound C_3P_4 , for which P_4 uniquely predicts the outcome. P_4 will be close to the asymptote of zero on these trials in the pattern-relevant group as it was consistently nonreinforced during training, but further away from asymptote in the colour-relevant group for which it was partially reinforced during training. According to the preceding interpretation of Rescorla's explanation, this arrangement should result in responding to C_3P_4 extinguishing more rapidly in the colour-relevant group than in the pattern-relevant group, when in fact the opposite result was observed.

However, the interpretation that Rescorla (2001) offered for his findings can still be reconciled with the results of Experiment 6. As C_3 is consistently nonreinforced for the colour-relevant group during training, at the onset of the test discrimination its associative strength will be close to zero and thus far from the asymptote set by food on the C_3P_3 trial type. Increments in the associative strength of C_3 will therefore proceed rapidly, and after a few trials of the test discrimination the associative strength of C_3P_4 will also be relatively high. As a result, this compound will elicit considerable conditioned responding, giving the impression that the colour-relevant group is slow to learn about this compound. In the pattern-relevant group, the associative strength of C_3 will be higher than in the colour-relevant group at the onset of the test discrimination due to its partial reinforcement during training, and learning about the association between this stimulus and reinforcement will proceed less rapidly. Responding to C_3P_4 is therefore predicted to weaken more rapidly in the pattern-relevant group than in the colour-relevant group.

Experiment 7 was designed to rule out these alternative interpretations of the preceding results. The design of this experiment is presented in Figure 5.1. Groups colour-relevant consistent and pattern-relevant consistent were analogous to the colour-relevant and pattern-relevant groups in Experiments 4 and 6, receiving training which involved one consistently relevant stimulus dimension, and another consistently irrelevant dimension. Two additional groups were included in Experiment 7: groups colour-relevant mixed and pattern-relevant mixed, for which two exemplars from the otherwise irrelevant dimension were relevant. The first column of Figure 5.1 shows the training trial types that were received by both colour-relevant groups, and those received by both pattern-relevant groups. Thus for groups colour-relevant consistent and colour-relevant mixed, colours C_1 , C_2 and C_3 were relevant, with C_1 and C_2 reliably signalling food and C_3 signalling the absence of food. Patterns P_1 , P_2 and P_3 were irrelevant, signalling food on 50% of presentations. For groups pattern-relevant consistent and pattern-relevant mixed, patterns P_1 , P_2 and P_3 were relevant, with P_1 and P_2 reliably signalling food and P_3 signalling the absence of food. Colours C_1 , C_2 and C_3 were irrelevant, signalling food on 50% of presentations.

The second and third columns of Figure 5.1 show four additional training trial types that were received by the consistent and mixed groups respectively. For the colour-relevant consistent group, the colours C_4 and C_5 were relevant to the outcome that followed them, and the patterns P_4 and P_5 were irrelevant. However for the colour-relevant mixed group, the colours C_4 and C_5 were irrelevant, and the patterns P_4 and P_5 were relevant, reliably signalling food and the absence of food respectively. For the pattern-relevant consistent group, the two patterns P_4 and P_5 were relevant to the outcome that followed them, and the colours C_4 and C_5 were irrelevant. However for the pattern-relevant mixed group, the patterns P_4 and P_5 were irrelevant and the colours which










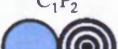
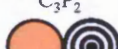

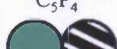


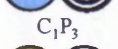
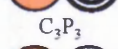








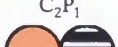
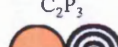
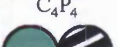

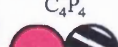
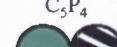
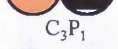
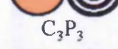


Training						Test			
	Both Groups		Consistent		Mixed		All Subjects		
	+	-	+	-	+	-	+	-	-
Colour-Relevant	 C ₁ P ₂	 C ₃ P ₂	 C ₄ P ₄	 C ₅ P ₄	 C ₄ P ₄	 C ₄ P ₅	 C ₁ P ₁	 C ₁ P ₂	 C ₂ P ₁
	 C ₁ P ₃	 C ₃ P ₃	 C ₄ P ₅	 C ₅ P ₅	 C ₅ P ₄	 C ₅ P ₅			
	 C ₂ P ₁	 C ₃ P ₁							
	 C ₂ P ₃	 C ₃ P ₃							
Pattern-Relevant	 C ₂ P ₁	 C ₂ P ₃	 C ₄ P ₄	 C ₄ P ₅	 C ₄ P ₄	 C ₅ P ₄			
	 C ₃ P ₁	 C ₃ P ₃	 C ₅ P ₄	 C ₅ P ₅	 C ₄ P ₅	 C ₅ P ₅			
	 C ₁ P ₂	 C ₁ P ₃							
	 C ₃ P ₂	 C ₃ P ₃							

Figure 5.1. Design of Experiment 7. The first column shows the trial types received by consistent and mixed subjects within the colour-relevant and pattern-relevant groups. In addition to these trial types, subjects received four more trial types which differed for the consistent and mixed subjects. After 32 sessions of training, all subjects received 12 sessions of the same test discrimination.

accompanied these stimuli, C_4 and C_5 , were relevant, reliably signalling food and the absence of food respectively.

During two sessions towards the end of training, each of the colours and patterns was tested individually. This was done to ensure that the discrimination training with the elements that were to be used for the test trials had been effective in both the consistent and the mixed groups. Following training, all four groups received a test discrimination in which a novel combination of two stimuli presented during training was reinforced (C_1P_1+), and two compounds that had been consistently reinforced for both groups were nonreinforced (C_1P_2- and C_2P_1-). Critically, the discrimination $C_1P_1+ C_1P_2-$ was based on two patterns that had been relevant for both pattern-relevant groups and irrelevant for both colour-relevant groups during training, and the discrimination $C_1P_1+ C_2P_1-$ was based on two colours that had been relevant for both colour-relevant groups and irrelevant for both pattern-relevant groups during training.

According to the principles of the theory of attention proposed by Mackintosh (1975a), attention will increase to the colours C_1 , C_2 , C_3 , C_4 and C_5 in the colour-relevant consistent group during training as all five of these colours are more accurate predictors of the outcome that follows them than the accompanying patterns P_1 , P_2 , P_3 , P_4 and P_5 . For the same reason, attention will increase to the patterns P_1 , P_2 , P_3 , P_4 and P_5 in the pattern-relevant consistent group. Thus on test, the colour-relevant consistent group should solve the discrimination based on the colours C_1 and C_2 ($C_1P_1+ C_2P_1-$) more rapidly than the pattern-relevant consistent group, and the pattern-relevant consistent group should solve the discrimination based on patterns P_1 and P_2 ($C_1P_1+ C_1P_2-$) more rapidly than the colour-relevant consistent group.

According to Mackintosh (1975a), in the colour-relevant mixed group, attention will increase to the colours C_1 , C_2 , and C_3 during training as these stimuli are better predictors of the outcome that follows them than the patterns P_1 , P_2 , and P_3 . However, for the same reason attention will also increase to the patterns P_4 and P_5 at the expense of C_4 and C_5 . In the pattern-relevant mixed group, attention will increase to the patterns P_1 , P_2 , and P_3 , and to the colours C_4 and C_5 . Mackintosh proposes that attention increases to specific stimuli, but can generalise to similar stimuli. Indeed, traditional demonstrations of the IDS effect (e.g. Mackintosh and Little, 1969) are explained by assuming that there is generalisation of attention from the initially relevant stimuli to novel exemplars from the same dimension that are presented on test. It follows from Mackintosh's theory that in the colour-relevant mixed group there will be generalisation of enhanced attention from the relevant patterns P_4 and P_5 to the other patterns, which should facilitate subsequent learning about P_1 and P_2 , which were irrelevant during training, when these patterns are presented at test. It also follows that the loss of attention to C_4 and C_5 , which were irrelevant during training, will generalise to C_1 and C_2 , which should disrupt subsequent learning about these stimuli. Similarly, in the pattern-relevant mixed group there will be generalisation of attention from C_4 and C_5 to the colours C_1 and C_2 , and the loss of attention to P_4 and P_5 will generalise to P_1 and P_2 .

It is therefore predicted that the mixed groups will acquire the discrimination based on previously irrelevant stimuli (C_1P_1+ C_1P_2- for the colour-relevant mixed group and C_1P_1+ C_2P_1- for the pattern-relevant mixed group) more readily than their consistent counterparts, but will be slower to acquire the discrimination based on relevant stimuli (C_1P_1+ C_2P_1- for the colour-relevant mixed group and C_1P_1+ C_1P_2- for the pattern-relevant mixed group). Generalisation is not expected to be complete.

Stimuli that received attention during training because they were relevant will therefore receive more attention on test than those irrelevant stimuli that have received generalised attention, with the result that the mixed groups are unlikely to acquire the test discrimination based on previously irrelevant stimuli as readily as that based on previously relevant stimuli.

The explanations based on the partial reinforcement extinction account and on Rescorla's (2001) rule generate a different prediction. Both accounts predict that the discrimination C_1P_1+ C_2P_1- should be acquired more rapidly by the colour-relevant groups than by the pattern-relevant groups, and that the discrimination C_1P_1+ C_1P_2- should be solved more rapidly by the pattern-relevant groups than by the colour-relevant groups, but that there will be no difference between the mixed and consistent groups on either discrimination. Consider the discrimination based on colours: C_1P_1+ C_2P_1- . During training the element C_2 , which is the distinctive feature of the test compound C_2P_1 , was consistently reinforced in both the colour-relevant consistent and colour-relevant mixed groups and was partially reinforced in both pattern-relevant groups. According to the partial reinforcement extinction account, this arrangement should lead to responding extinguishing at a comparable rate in the two colour-relevant groups, which will be faster than that in the two pattern-relevant groups. According to the account based on the Rescorla (2001) rule, responding will extinguish more quickly to C_2P_1 in the two colour-relevant groups because the distinctive feature C_2 will be further away from asymptote in these two groups than in the pattern-relevant groups. The same logic can be applied to the discrimination based on patterns. Responding should extinguish more quickly to C_1P_2 in the two pattern-relevant groups than in the two colour-relevant groups due to the consistent reinforcement of P_2 in the former group (which ensures that it is far from asymptote

on test) and the partial reinforcement of this stimulus in the latter (which ensures that it is close to asymptote on test).

Experiment 7

Method

Subjects. The subjects were 56 experimentally naïve adult homing pigeons.

They were fed and maintained in the same manner as subjects in Experiments 4 and 6.

Apparatus. The apparatus was the same as that used in Experiments 4 and 6.

The same stimuli were used, but in this experiment there were five colours: cyan, yellow, orange, magenta and green (represented by C₁, C₂, C₃, C₄ and C₅ respectively for all subjects), and five patterns. Four of the patterns were the same as those used in Experiments 4 and 6: stripes with orientations 90°, 0°, 45° or -45° (represented by P₁, P₂, P₄ and P₅ respectively for all subjects). The other pattern, P₃, consisted of three white circular bands, each with a width of 2 mm. The outermost band formed a circle with diameter 2.4 cm. Each band was separated by black circular bands of the same width. In the centre of the stimulus was a black circle (diameter 4 mm).

Procedure. 14 pigeons were assigned to each of the four groups: colour-relevant consistent, colour-relevant mixed, pattern-relevant consistent and pattern-relevant mixed. Magazine training and autoshaping proceeded in the same manner as in Experiment 6. Session 1 of training began on the day after the final session of autoshaping. During each of the 32 sessions of this stage, subjects received the training trial types summarised in Figure 5.1. There were 48 trials in each session. Each of the 11 different compounds was presented four times in each session, with the exception of the nonreinforced compound C₃P₃, which was presented eight times in each session.

On Sessions 27 and 30 of training, subjects received 43 training trials which were intermixed with 5 trials on which a single circle, containing one of the colours or patterns used in training, was presented either where the left-hand circle of the training compounds appeared, or where the right-hand circle appeared. For half of the animals within each of the four groups, the five colours used during training were presented individually during session 27, and the five patterns used in training were presented individually during session 30. For the other half, the patterns were tested during session 27 and the colours were tested during session 30. All of these trials were nonreinforced.

The test phase began on the day following the final session of training. During the 12 sessions of this test phase, subjects received two compounds that had been reinforced during training; C_1P_2 and C_2P_1 . These compounds were each presented 10 times in every session and were nonreinforced. 20 reinforced presentations of C_1P_1 , a novel combination of two stimuli presented during training, were intermixed with the nonreinforced trial types on each session. All other procedural details that have been omitted were the same as in Experiments 4 and 6.

Results

The mean rate of responding during presentations of the six reinforced compounds was calculated for each subject for every session of training, and the same was done for the six nonreinforced compounds. For clarity of presentation, the data for the two colour-relevant groups are presented in the upper panel of Figure 5.2, and were analysed separately from the data for the two pattern-relevant groups, which are presented in the lower panel of this figure. From the upper panel of Figure 5.2 it appears that the colour-relevant consistent group acquired the discrimination between

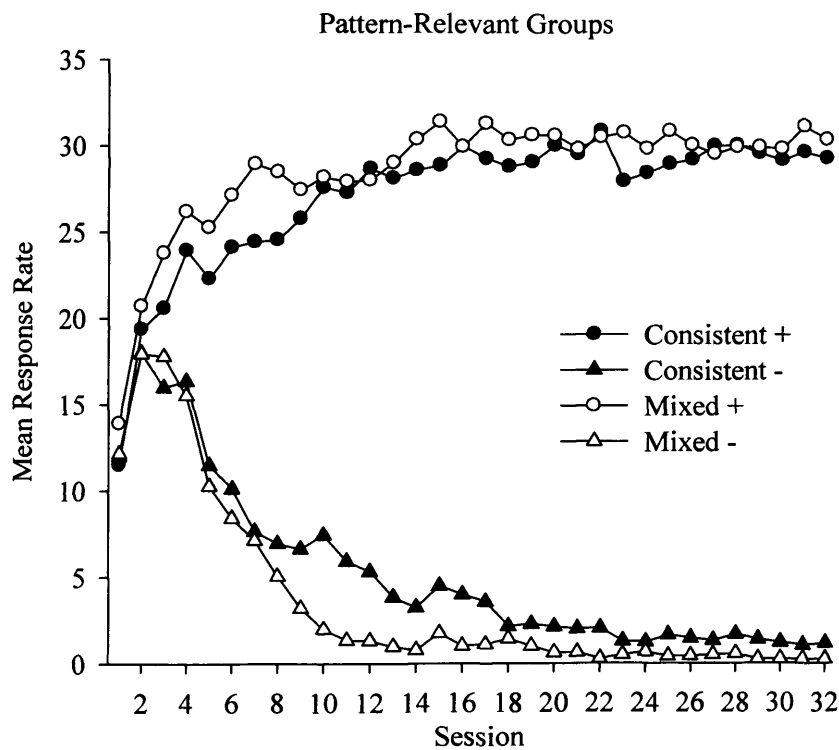
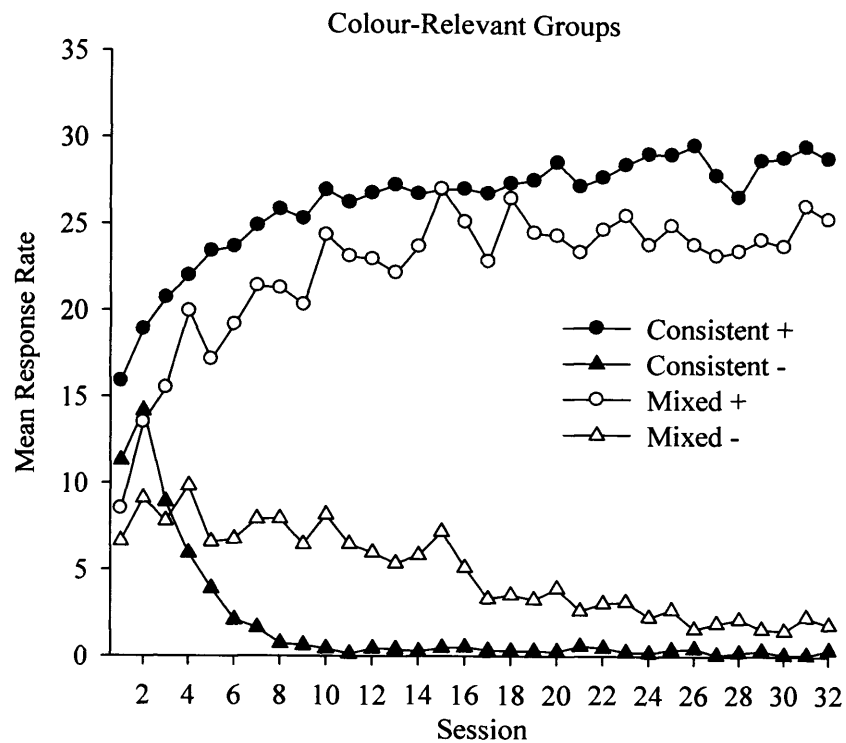


Figure 5.2. The mean rate of responding during reinforced and nonreinforced trials during training for the consistent and mixed colour-relevant groups (upper panel) and for the consistent and mixed pattern-relevant groups (lower panel) in Experiment 7.

the reinforced and nonreinforced trial types more readily than the colour-relevant mixed group. This difference presumably reflects that fact that the colour-relevant mixed group were slow to discriminate between the four trial types they received for which patterns were relevant. A three-way analysis of variance (ANOVA) of individual mean response rates during presentations of each trial type was conducted, with the factors of group (colour-relevant consistent or mixed), trial type (reinforced and nonreinforced) and session, for the 32 sessions of training. The results from this ANOVA revealed that there was no significant effect of group, $F < 1$. However, there was a significant effect of trial type, $F(1, 26) = 297.13$, $MSE = 669.45$, and session, $F(31, 806) = 1.96$, $MSE = 19.57$, a significant Group x Trial Type interaction, $F(1, 26) = 8.07$, $MSE = 669.45$, Group x Session interaction, $F(31, 806) = 2.81$, $MSE = 19.57$, Trial Type x Session interaction, $F(31, 806) = 44.39$, $MSE = 11.42$, and Group x Trial Type x Session interaction, $F(31, 806) = 1.85$, $MSE = 11.42$.

The three-way interaction was analysed using simple main effects tests, which revealed that there was a significant effect of trial type from Session 1 onwards in the consistent group, $F_s(1,832) > 4.60$, $MSE = 31.98$, and from Session 2 onwards in the mixed group, $F_s(1,832) > 4.22$, $MSE = 31.98$. The consistent group responded at a higher rate in the presence of reinforced trial types than the mixed group on sessions 1, 2, 3, 5, 9, 13, 24, 26, 27 and 30, $F_s(1,1664) > 3.89$, $MSE = 39.16$, and at a significantly lower rate than the mixed group during nonreinforced trial types on sessions 1, 2 and 6 to 15 inclusive, $F_s(1,1664) > 3.89$, $MSE = 39.16$. Although there were differences between the two groups over the course of training, by the final sessions these differences were no longer statistically significant during both the reinforced and nonreinforced trial types.

From the lower panel of Figure 5.2 it appears that unlike the two colour-relevant groups, the pattern-relevant consistent group and pattern-relevant mixed group acquired the discrimination between the reinforced and nonreinforced trial types at a similar rate. Thus, it appears that as patterns were relevant for the majority of the trial types received by the pattern-relevant mixed group, they readily learned to discriminate between these trial types, but they were also quick to discriminate between the four trial types for which colours were relevant. A three-way analysis of variance (ANOVA) of individual mean response rates during presentations of each trial type was conducted, with the factors of group (pattern-relevant consistent or mixed), trial type (reinforced and nonreinforced) and session, for the 32 sessions of training. The results from this ANOVA revealed that there was no significant effect of group, $F < 1$. There was a significant effect of trial type, $F(1, 26) = 152.83$, $MSE = 1604.37$, and session, $F(31, 806) = 7.69$, $MSE = 15.44$, and a significant Trial Type x Session interaction, $F(31, 806) = 79.07$, $MSE = 12.66$. The Group x Session interaction was not significant, $F(31, 806) = 1.13$, $MSE = 15.44$, along with the Group x Trial Type and Group x Trial Type x Session interactions, $F_s < 1$. The Trial Type x Session interaction was analysed using simple main effects tests, which revealed that there was a significant effect of trial type from Session 3 onwards $F_s(1, 832) > 6.30$, $MSE = 62.40$.

Responding to individual stimuli presented during Sessions 27 and 30 of training is shown in Figures 5.3 and 5.4 for the four groups. Figure 5.3 shows responding to the elements that were both consistently reinforced during training and presented on test (C_1 and C_2 for the two colour-relevant groups, P_1 and P_2 for the two

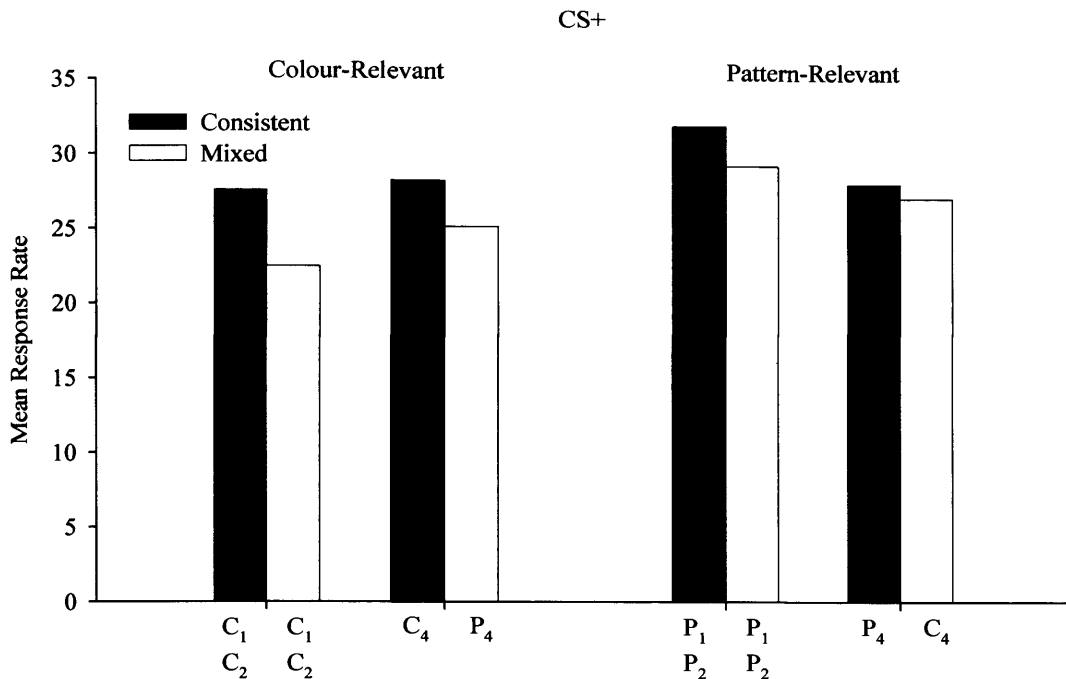


Figure 5.3. The mean rate of responding during Sessions 27 and 30 of training in Experiment 7 to individual elements that had been reinforced during training for the four groups.

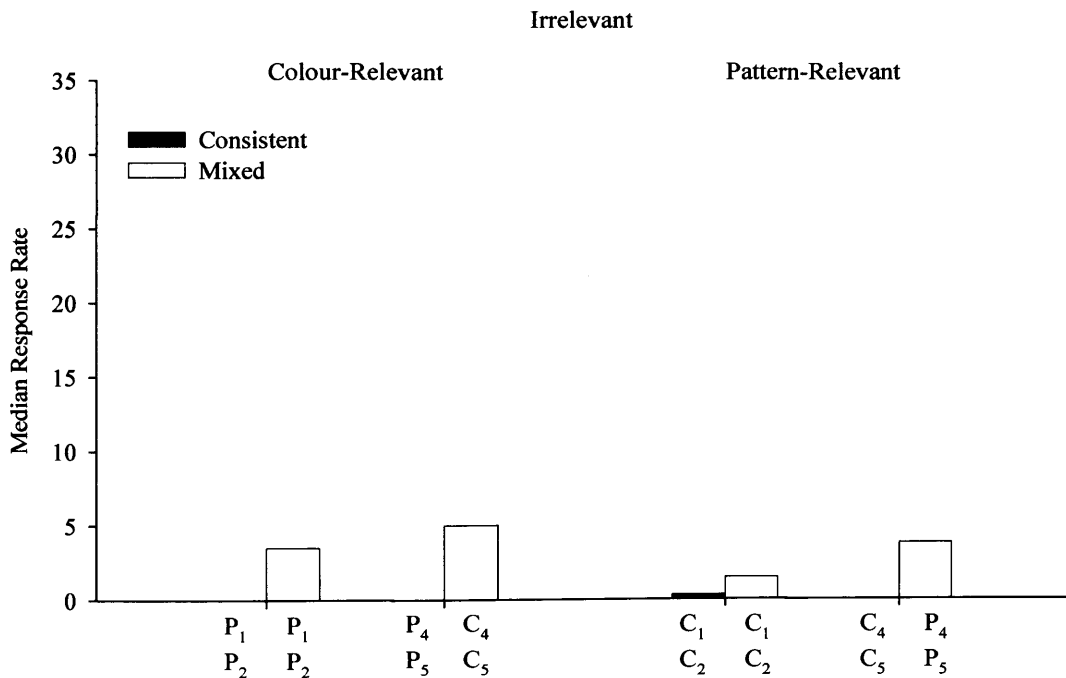


Figure 5.4. The median rate of responding during Sessions 27 and 30 of training in Experiment 7 to individual elements that had been irrelevant during training for the four groups.

pattern-relevant groups), and responding to the other elements that were reinforced during training (C₄ for groups colour-relevant consistent and pattern-relevant mixed, and P₄ for groups colour-relevant mixed and pattern-relevant consistent). From this figure it is evident that the four groups responded at a high rate to all stimuli that had been reinforced during training. A three-way ANOVA of individual mean responses made during presentations of these trial types was conducted, with the factors of group (pattern-relevant or colour-relevant) consistency (consistent or mixed), and stimulus (test and other). This analysis revealed no effect of group, consistency or stimulus $F_s < 1$, and no Group x Trial Type interaction, $F(1, 52) = 3.49$, $MSE = 43.91$. None of the other interactions was significant, $F_s < 1$.

Figure 5.4 shows responding to elements that had been irrelevant during training and were presented on test (P₁ and P₂ for both colour-relevant groups, and C₁ and C₂ for the pattern-relevant groups), and responding to other elements that had been irrelevant during training (P₄ and P₅ for groups colour-relevant consistent and pattern-relevant mixed, and C₄ and C₅ for groups colour-relevant mixed and pattern-relevant consistent). As a result of the large number of pigeons that responded at a rate of zero during presentations of individual irrelevant stimuli, the group median response rates for these stimuli are shown in Figure 5.4. Mann-Whitney U tests revealed that during presentations of irrelevant stimuli that did not appear on test the colour-relevant mixed group responded at a higher rate to C₄ and C₅ than the colour-relevant consistent group did to P₄ and P₅, $U(14, 14) = 19.50$, and the pattern-relevant mixed group responded at a higher rate to P₄ and P₅ than the pattern-relevant consistent group did to C₄ and C₅, $U(14, 14) = 31.50$. The important comparisons however are between the groups in their responding to the irrelevant elements involved in the test discrimination. Mann-Whitney U tests revealed that although

there was no significant difference between the two pattern-relevant groups for these elements (C_1 and C_2), $U(14, 14) = 78.00$, there was a significant difference between the colour-relevant groups for these elements (P_1 and P_2), $U(14, 14) = 48.00$. It should be noted that although statistically significant, the numerical difference between the two groups in their responding to these stimuli was only slight, especially when the high rate of responding observed in the presence of the reinforced elements is considered. The mean rate of responding during individual presentations of the two elements that were consistently nonreinforced during training was less than one in all four groups.

The mean response rate during presentations of the reinforced compound C_1P_1 across the 12 sessions of the test phase combined was 29.83 for the colour-relevant consistent group, 24.76 for the colour-relevant mixed group, 29.47 for the pattern-relevant consistent group and 29.49 for the pattern-relevant mixed group. A two-way ANOVA of individual mean number of responses made in the presence of C_1P_1 , with the factors of group (colour-relevant consistent, colour-relevant mixed, pattern-relevant consistent and pattern-relevant mixed) and session, revealed that there was a significant effect of session, $F(11, 572) = 20.32$, $MSE = 21.33$, but no effect of group, $F < 1$ and no Group x Session interaction, $F(33, 572) = 1.25$, $MSE = 21.33$.

Discrimination ratios were calculated for the test discrimination based on patterns (C_1P_1+ C_1P_2-) and the test discrimination based on colours (C_1P_1+ C_2P_1-). These ratios were of the form $Y/(Y+X)$, where X represented the mean response rate during presentations of the reinforced compound (C_1P_1) and Y represented the mean response rate during presentations of the nonreinforced compound (C_1P_2 or C_2P_1). A ratio of 0.5 therefore indicates that subjects failed to discriminate between the compounds, and a ratio of 0.0 indicates a perfect discrimination between them. These

ratios, calculated for each of the 12 sessions of the test phase, are presented in Figure 5.5.

The upper panel of this figure shows the results from the component of the test discrimination for which patterns were the relevant features. Inspection of this figure reveals that the pattern-relevant consistent group solved the discrimination based on patterns more readily than the colour-relevant consistent group, which had not acquired the discrimination by the end of the test phase. The colour-relevant mixed group acquired the discrimination more rapidly than the colour-relevant consistent group. The pattern-relevant mixed group was slower to acquire the discrimination than the pattern-relevant consistent group, but more rapid than the colour-relevant mixed group. The lower panel of Figure 5.5 shows the results from the component of the test discrimination for which colours were the relevant features. In keeping with previous results, inspection of this figure suggests that although all groups acquired the discrimination based on colours fairly rapidly, the colour-relevant consistent group acquired it more rapidly than the pattern-relevant consistent group. The colour-relevant mixed group acquired the discrimination more slowly than the colour-relevant consistent group, but more quickly than the pattern-relevant mixed group. This latter group appeared to solve the discrimination more quickly than the pattern-relevant consistent group.

A four-way ANOVA was conducted on the individual mean discrimination ratios during each session of the test with the factors of group (colour-relevant or pattern-relevant), consistency (consistent or mixed), discrimination (C_1P_1+ C_1P_2- and C_1P_1+ C_2P_1-) and session. This analysis revealed a significant effect of group, $F(1, 52) = 7.95$, $MSE = 0.11$, discrimination, $F(1, 52) = 58.96$, $MSE = 0.01$, and session, $F(11, 572) = 214.98$, $MSE = 0.01$. The effect of consistency, the Consistency x Group

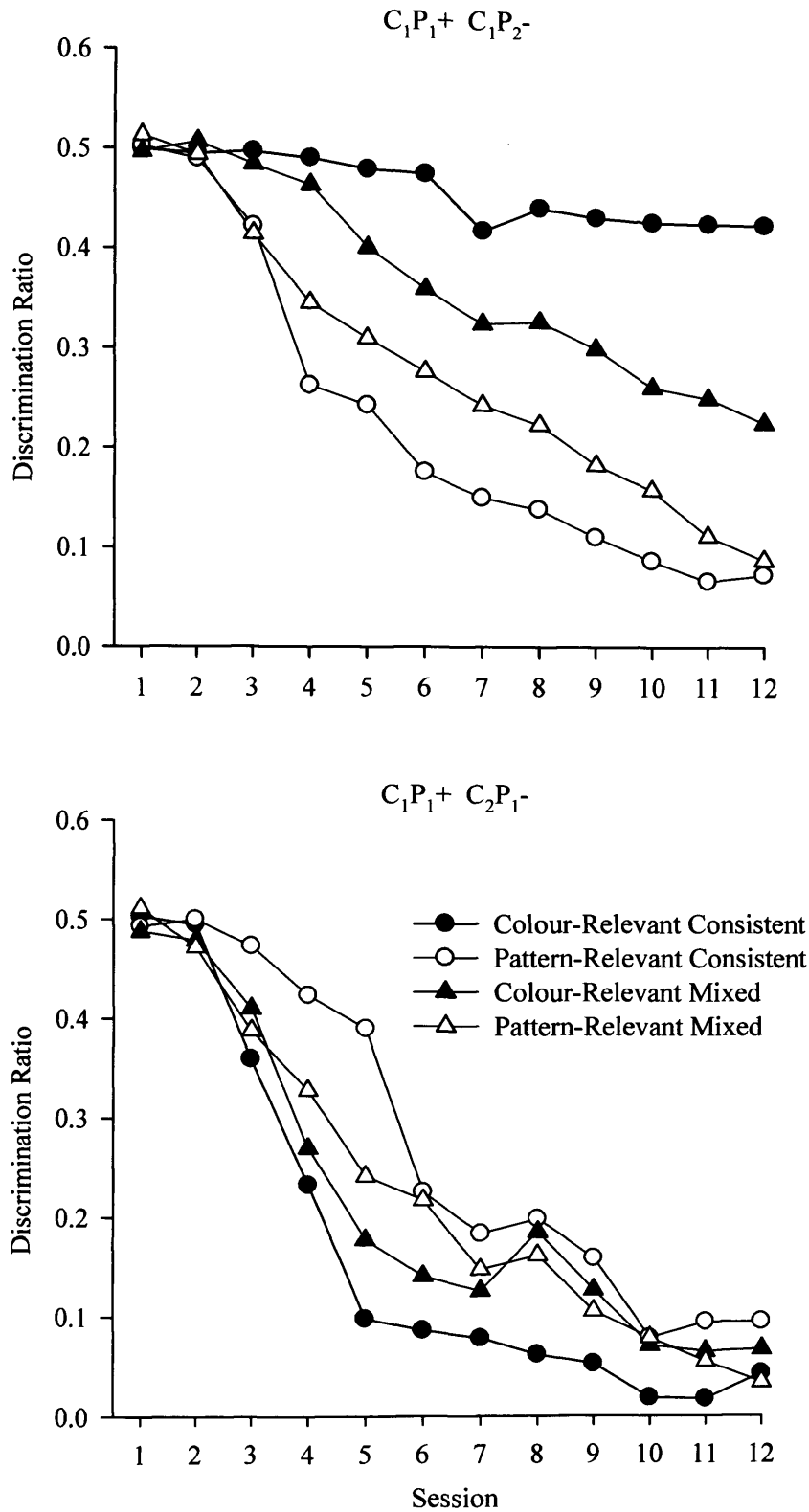


Figure 5.5. The mean discrimination ratios for the four groups for each session of the test phase during Experiment 7, for the discrimination where patterns were relevant (upper panel) and the discrimination where colours were relevant (lower panel).

and the Consistency x Discrimination interactions were not significant $F_s < 1$, along with the Consistency x Session and Consistency x Group x Session interactions, $F_s(11, 572) < 1.78$, $MSE = 0.01$. The Group x Discrimination and Consistency x Group x Discrimination interactions were significant, $F_s(1, 52) > 17.52$, $MSE = 0.07$, as were each of the other interactions, $F_s(11, 572) > 2.22$, $MSE = 0.01$, including the Consistency x Group x Discrimination x Session interaction. This four-way interaction was analysed further using simple main effects tests.

For the discrimination that was based on patterns (C_1P_1+ C_1P_2-), these tests revealed that the pattern-relevant consistent group performed better than the colour-relevant consistent group on Sessions 4 to 12, $F_s(1, 1248) > 24.83$, $MSE = 0.01$, and the pattern-relevant mixed group performed better than the colour-relevant mixed group on Sessions 8 to 12, $F_s(1, 1248) > 4.99$, $MSE = 0.01$. The colour-relevant mixed group acquired the discrimination more readily than the colour-relevant consistent group, with a significant difference between these two groups on Sessions 6 to 12, $F_s(1, 1248) > 4.12$, $MSE = 0.01$. The pattern-relevant consistent group performed better than the pattern-relevant mixed group on Sessions 6 and 7, $F_s(1, 1248) > 4.12$, $MSE = 0.01$.

Turning now to the discrimination that was based on colours (C_1P_1+ C_2P_1-), the colour-relevant consistent group outperformed the pattern-relevant consistent group on Sessions 3 to 9, $F_s(1, 1248) > 5.20$, $MSE = 0.01$, but the two mixed groups did not differ on any session. The colour-relevant consistent group was only significantly better than the colour-relevant mixed group on Session 8, $F(1, 1248) = 7.30$, $MSE = 0.01$, and the pattern-relevant mixed group was better than the pattern-relevant consistent group on Sessions 4 and 5, $F_s(1, 1248) > 4.32$, $MSE = 0.01$.

Discussion

The results of Experiment 7 confirmed the findings reported in Experiments 4 and 6 that when pigeons received discrimination training in which one stimulus dimension was relevant and another irrelevant, learning about previously relevant stimuli during a subsequent test discrimination was facilitated relative to learning about previously irrelevant stimuli. This experiment extended the results of the preceding experiments by demonstrating that if two exemplars from the otherwise irrelevant dimension are relevant during training, subsequent learning about irrelevant stimuli is facilitated.

A potential caveat in drawing this conclusion is the finding that when the individual elements were tested towards the end of training, a significant difference was found in the rate at which the two colour-relevant groups responded to elements that were irrelevant during training. It could be argued that the different rate at which the consistent and mixed colour-relevant groups acquired the test discrimination based on previously irrelevant stimuli, C_1P_1+ C_1P_2- , was in fact an artefact of this difference. However, considering the very low rate of responding to P_1 and P_2 in the colour-relevant mixed group, and the extent of the difference observed between this group and the colour-relevant consistent group on test, this interpretation can hardly be justified. Furthermore, no such explanation can apply to the two pattern-relevant groups, where there was no hint of a difference between the rates of responding during individual presentations of the irrelevant elements C_1 and C_2 , and yet the C_1P_1+ C_2P_1- discrimination was acquired significantly more rapidly by the pattern-relevant mixed group than the pattern-relevant consistent group.

The results of Experiment 7 cannot be explained by appealing to the partial reinforcement extinction effect, or the rule devised by Rescorla (2001), which were

discussed in the introduction to this chapter. Both of these interpretations predict that whether one dimension was consistently relevant and one irrelevant, or both were partially relevant during training, should have no impact on the test discrimination. In both cases the distinctive feature within each of the nonreinforced compounds had received the same reinforcement schedule during training. An account based on the partial reinforcement extinction effect therefore predicts that responding during the test phase should have been unaffected whether consistent or mixed training had been given. According to the explanation based on Rescorla's rule, where the distinctive cue had been relevant during training, it had previously been consistently reinforced in the consistent and the mixed group, and thus should be equally distant from asymptote on test, resulting in rapid learning about the compound. Where the distinctive cue had been irrelevant during training, it had previously been partially reinforced in the consistent and the mixed group, and thus should be equally close to asymptote on test, resulting in all subjects learning relatively more slowly about this compound.

The current findings also provide a further reason for rejecting the orienting responses account that was offered as an explanation for the results of Experiment 4. Again this account does not predict that there will be a difference on test between the consistent and mixed groups, as in both cases the distinctive cues within each compound were associated with food to the same extent. For all subjects the distinctive feature that had been relevant during training should elicit strong orienting responses as it was consistently followed by food, and the distinctive feature that had previously been irrelevant should elicit relatively weaker orienting responses as it was followed by food just 50% of the time during training. Thus learning about previously relevant stimuli should have proceeded equally rapidly in the consistent and mixed

groups, and learning about previously irrelevant stimuli should have proceeded at a rate that was similar for both groups.

In Chapter 3, it was argued that an explanation proposed by Hall (1991) in terms of acquired equivalence was unable to account for the findings of Experiments 4 and 5. Specifically, Hall proposed that by virtue of signalling the same outcome, irrelevant stimuli are treated as equivalent during true discrimination learning. In contrast, stimuli from the relevant dimension signal different outcomes and become easier to distinguish. This account could not predict the finding in Experiment 4 that two stimuli that had both been consistently reinforced during training were distinguished with ease during the test discrimination.

The results from Experiment 4 may, however, be explained by a slightly different account to that suggested by Hall (1991). According to Gibson (1940), if two stimuli are differentially reinforced, their generalisation gradients will be steepened. Although the mechanism responsible for steepening these gradients was not specified, the idea is nevertheless plausible and warrants consideration. Consider the colour-relevant consistent group of Experiment 7, which is analogous to the colour-relevant group in Experiment 4. For this group, colours C_1 and C_2 signalled the same outcome during training, reinforcement. These two stimuli will be differentiated from the colour C_3 , for example, which signalled nonreinforcement during training. As a result, the generalisation gradients of both C_1 and C_2 will be steepened and the test discrimination based on these stimuli (C_1P_1+ C_2P_1-) should be acquired with ease. In contrast, the irrelevant stimuli P_1 and P_2 will not be differentiated from other patterns during training as each signalled food 50% of the time, and thus the subsequent test discrimination based on these stimuli will proceed with difficulty. For the colour-relevant mixed group in Experiment 7, exemplars from the same dimension as the

irrelevant stimuli presented on test are followed by different outcomes during training. Specifically, P_1 , P_2 and P_3 are followed by food on 50% of presentations, P_4 is consistently reinforced and P_5 is consistently nonreinforced. Having differentiated P_1 , P_2 and P_3 from P_4 and P_5 during training, the generalisation gradients of these patterns should be steepened. Thus on test, the colour-relevant mixed group should acquire the discrimination based on patterns (C_1P_1+ C_1P_2-) more readily than the colour-relevant consistent group.

Despite its ability to account for the difference observed between the mixed and consistent groups for the discrimination based on previously irrelevant stimuli, the differentiation account does not anticipate the difference observed between the consistent and mixed groups for the test discrimination based on previously relevant stimuli. For both of these groups, the previously reinforced stimuli on which this discrimination is based should have been differentiated from the nonreinforced stimuli during training, with their generalisation gradients being steepened to an equal extent. Thus this discrimination should have been acquired at an equivalently rapid rate in both the consistent and mixed groups when in fact the mixed groups were slower to acquire it than the consistent groups.

Having ruled out a number of alternative interpretations as satisfactory explanations for the results of Experiment 7, I turn now to considering the theory of attention proposed by Mackintosh (1975a). According to Mackintosh, when one dimension is consistently relevant, attention should increase to all of the trained exemplars from that dimension during training, by virtue of these stimuli being the most accurate predictors of the outcome. All trained exemplars from the other, irrelevant dimension will lose associability. These changes in attention will result in a subsequent test discrimination based on previously relevant stimuli being acquired

more readily than one based on previously irrelevant stimuli. This explanation accounts for the results reported in the preceding chapters, as well as the differences observed between the colour-relevant consistent and pattern-relevant consistent groups in the current experiment.

According to Mackintosh (1975a), attention generalises from one stimulus to another as a function of the similarity between the two. It follows from this account that in the mixed groups in Experiment 7, attention generalised from the two relevant exemplars of the otherwise irrelevant dimension to the irrelevant stimuli used on test. Such generalisation can explain the fact that these groups learned the test discrimination based on previously irrelevant stimuli more rapidly than the consistent groups. The finding that the mixed groups acquired the test discrimination based on previously relevant stimuli more slowly than the consistent groups can also be explained. Consider the colour-relevant mixed group. In this group, enhanced attention to the relevant patterns P_4 and P_5 during training is expected to generalise to the irrelevant patterns P_1 and P_2 , facilitating the subsequent test discrimination based on these stimuli. However, a loss of attention to the colours C_4 and C_5 , which are irrelevant during training, should generalise to the relevant colours C_1 and C_2 . Thus on test, the colours C_1 and C_2 will receive less attention in the mixed group than in the consistent group, for which all colours were relevant during training, and the discrimination C_1P_1+ C_2P_1- will not be acquired as readily by the former group as by the latter.

Although Mackintosh's (1975a) theory provides a convincing explanation for the results of Experiment 7, it should be noted that accepting this interpretation seems to require the assumption that there is generalisation of attention between stimuli that can clearly be discriminated on the basis of differing associative strength. The tests of

the individual stimuli administered near the end of training revealed that subjects showed a large difference in their responding to features that were relevant during training and those that were irrelevant. By way of example, consider the test discrimination based on previously irrelevant patterns for the two colour-relevant groups: C_1P_1+ C_1P_2- . To explain the superior performance of the mixed group, it must be assumed that attention generalised from the two patterns that were relevant during training (P_4 and P_5) to the two previously irrelevant patterns that were presented on test P_1 and P_2 . However, there was no evidence from the tests of the individual elements that there was generalisation of associative strength between these stimuli. Ideally, the assumption that attention generalises between stimuli needs to be justified by the development of rules that specify the degree to which such generalisation occurs.

Most demonstrations of the IDS/EDS effect, as well as the results reported in Chapters 3 and 4, can be explained if it is assumed that rather than attention being established to specific stimuli during training and generalising, it is established to certain stimulus dimensions. One such interpretation is offered by the theory of attention proposed by Sutherland and Mackintosh (1971). This theory is a two-process model in which animals first learn to attend to the relevant stimulus dimension, and then attach the correct responses to different stimuli along this dimension. According to this view, the stimulus input is fed to a number of analyzers, each of which classifies stimuli along a dimension. Each exemplar from that dimension (such as horizontal or vertical along the orientation analyzer) is then attached to a response (e.g. approach or avoid). Changes in attention are represented by changes in the strengths of various analyzers. An analyzer is strengthened at the expense of all others when its exemplars accurately predict an outcome, and that strength in turn

determines how much is learned about a particular stimulus-response connection.

Each analyzer detects variations along a particular stimulus dimension, thus when the strength of the analyzer increases, attention increases to the whole stimulus dimension, rather than to specific stimuli along that dimension.

Applying this reasoning to Experiment 7, in the mixed groups, attention should increase to the dimensions of both colour and pattern during training as some exemplars from each of these dimensions are relevant. As a result, these groups should acquire the test discrimination based on either dimension readily. However, it might be expected that the more exemplars from a given dimension are relevant, the greater extent to which the analyzer for that dimension is strengthened. In the mixed groups, the test discrimination based on previously relevant stimuli involved discriminating stimuli from the dimension from which four stimuli were relevant during training. The analyzer for this dimension will not have as much strength as when all six of the exemplars from that dimension were previously relevant, which could account for the observed difference between the mixed and consistent groups in the rate at which the test discrimination based on previously relevant stimuli was acquired.

Few experiments have looked at whether changes in attention are dimensional or stimulus-specific, although the results of some IDS/EDS experiments have proved difficult to interpret in terms of attention being directed towards an entire dimension. For example, Dias, Robbins and Roberts (1996) trained monkeys with compounds that consisted of a black line superimposed on a blue polygon. Two compounds were presented simultaneously, one reinforced and the other nonreinforced, and monkeys learned that either the shape of the blue polygon or the shape of the black line was relevant to reward. The subsequent IDS/EDS effect that was observed could be

explained in terms of learning to attend to specific exemplars from a single dimension (different shapes) or to complex dimensions that represent combinations of colour and shape (the 'blue polygon' dimension, or the 'black line' dimension). Whether it is reasonable to assume that such complex dimensions exist is arguable.

Trobalon et al. (2003) conducted a series of experiments which involved rats trained in a radial arm maze to test the notion of whether attention is stimulus-specific or established to an entire dimension. The design of one experiment is presented in Figure 5.6. In Experiment 1, IDS subjects received a discrimination in which arm direction was relevant, such that the arm pointing north was reinforced consistently, and either the arm pointing east or the arm pointing west was nonreinforced. The floor covering in these arms (wood or plastic) was irrelevant, signalling reinforcement and nonreinforcement equally. For an EDS group, the same three arms were used, but floor covering was relevant and direction was irrelevant. The IDS group in Experiment 2 received a discrimination in which direction was again relevant. In this case, the arm pointing south was consistently reinforced, whereas either east or west was nonreinforced. For the EDS group in Experiment 2 the same three arms were used but direction was irrelevant and texture was relevant. A subsequent transfer discrimination involved the south-east and south-west arms for all subjects in both experiments. Arm direction was relevant to this discrimination, with one of these arms being reinforced and the other nonreinforced, and floor covering was irrelevant.

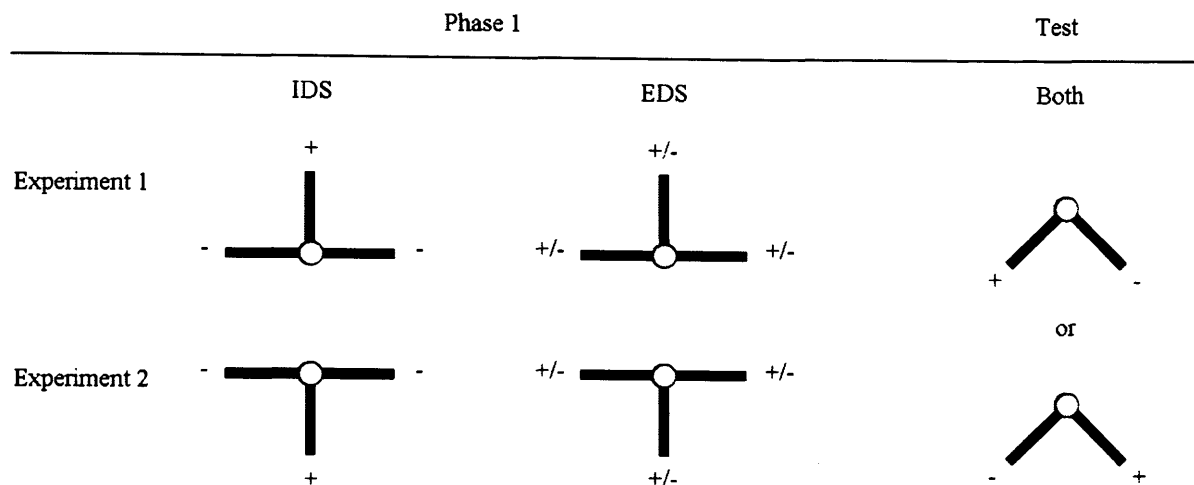


Figure 5.6. Schematic diagram of the layout of the maze in both phases of experiments by Trobalon et al. (2003).

Trobalon et al. (2003) found that in Experiment 1, the IDS group acquired the new spatial discrimination faster than the EDS group, a result which can be explained readily both by the theory of Sutherland and Mackintosh (1971) and by the theory of Mackintosh (1975a). According to the former, an increase in attention to the dimension of spatial direction will be established during training, which will facilitate learning of the test discrimination in the IDS group. According to the latter, attention will increase to the specific arm directions involved in training, and generalise to the novel arm directions used on test. These two interpretations were distinguished by the results of Experiment 2. Trobalon et al. observed that in this experiment, the IDS group were in fact slower to solve the test discrimination than the EDS group, that is, the reverse of the IDS/EDS effect was found. If the IDS animals had learnt to attend to the dimension of spatial direction as proposed by Sutherland and Mackintosh, they should have acquired the test discrimination more readily than the EDS animals. However, these results can be reconciled with Mackintosh's theory.

Trobalon et al. (2003) suggested that during Phase 1, IDS animals might have learned to attend to specific landmarks present in the test room that defined the locations of the reinforced and nonreinforced arms, whilst learning to ignore irrelevant landmark cues. An irrelevant landmark might, for example, constitute an object that was midway between the reinforced and nonreinforced arms. This landmark would be visible from both the reinforced and nonreinforced arm and thus would not enable the animal to differentiate these two arms. For the IDS subjects in Experiment 2, the irrelevant landmarks are those that define the positions of south-west or south-east; precisely the landmarks that define the position of the arms used in the test discrimination. If the animals had learned not to attend to these irrelevant cues during Phase 1, they should find the test discrimination in which they are relevant difficult, which is what Trobalon et al. (2003) observed. The EDS animals might have found this discrimination relatively easier as they had not learned to ignore specific arm directions. Thus rather than being established to an entire stimulus dimension, there is evidence that attention is stimulus-specific.

Finally, it should be noted that the theory of Mackintosh (1975a) has the potential to account for the effect that prompted Rescorla (2001) to develop the distance-from-asymptote rule. Consider again the experiment detailed in Table 5.1, in which stimuli A, B, C and D were pre-exposed before conditioning with A and C. The compound AB was then either reinforced or nonreinforced. According to Mackintosh's principles, the associative change undergone by A and B during compound training depends on the discrepancy of each element from asymptote. As a result of the conditioning phase, A will have high associative strength at the onset of this phase. When AB is reinforced during the compound training stage, as a poor predictor of the outcome, B will lose associability and increments in its associative

strength will be small. However, although attention will be paid to A, as a good predictor of the outcome, as a result of the conditioning phase the associative strength of this stimulus will be close to asymptote. Hence, any increments in associability will have little impact on increments in the associative strength of A. Essentially, therefore, the associability component of Mackintosh's model will have little impact during compound training, and increases in the associative strength of the separate elements will be determined predominantly by the error term. As its error term is large, B will gain a lot of associative strength during AB+ training. Thus when BC and AD are presented at test, owing to the prior conditioning with C, the overall associative strength of BC will be higher than that of AD, and this compound should elicit more responding.

Similarly, when AB is nonreinforced during compound training, more attention will be paid to B, a better predictor of the absence of the outcome, than A, but there will be little change in the associative strength of B as it is already close to asymptote. The error term for A on the other hand will be large, allowing this stimulus to lose associative strength as compound conditioning progresses. Thus, on test, the associative strength of both A and B will be close to zero on test, but C will have more associative strength than D. As a result, BC should again elicit more responding than AD.

The theory of attention proposed by Mackintosh (1975a) has been the focus of this and the preceding two chapters, because of the theories considered thus far it has proved to be the most successful in accounting for the results I have reported. Whilst these results imply the necessity for an attentional mechanism to be included in an all encompassing theory of learning, it is not claimed that Mackintosh's theory represents such a theory. Indeed, some of its weaknesses were discussed in Chapter 1. Thus

although Mackintosh's theory provides a suitable explanation for the results reported in this thesis, it is likely that a hybrid model is required if the fate of irrelevant stimuli in every circumstance is to be explained. Several theories of this kind have been developed, and in the final chapter I shall describe and evaluate two of them.

6. General Discussion

Summary

The aim of the experiments reported in this thesis was to discover the fate of irrelevant stimuli during discrimination learning. This aim was achieved through the use of variations of two established paradigms within the animal learning literature, blocking and simple discrimination learning of the kind AX+ BX-.

The aim of Chapter 2 was to determine whether the assumption that little is learned about irrelevant stimuli is valid, or whether learning occurs but is not expressed. The design of these experiments was based on the standard blocking procedure, in which A+ trials precede training with AX+, followed by a test of X alone. In the first of these experiments, A was extinguished following this treatment and a second test of X was then administered. The Rescorla-Wagner (1972) model (along with Mackintosh, 1975a; Pearce and Hall, 1980), predicts that little will be learned about X during compound conditioning, as the outcome is fully predicted by A. There will be no learning about X on the subsequent A- trials, and hence it should elicit little responding on both tests. In contrast, the comparator hypothesis predicts that the A-US association, established during initial training and strengthened during AX+ training, will prevent the expression of the X-US association during the initial test. However weakening the A-US association through extinction of A should allow X to elicit responding on the second test. The results of this experiment, and two variations on the design, were consistent with the Rescorla-Wagner model, and hence other theories (e.g. Mackintosh, 1975a; Pearce & Hall, 1980) that are based on the fundamental assumption that animals learn rather little about irrelevant stimuli.

The aim of Chapters 3, 4 and 5 was to evaluate the proposal that stimuli that have been irrelevant are learned about slowly in a new test because animals pay little attention to them. A novel variation of the simple discrimination procedure used by Wagner et al. (1968) was the basis for each of the experiments reported in these chapters. Thus, discrimination training of the sort: AX+ BX-, AY+ BY- was given, for which the stimuli A and B were accurate predictors of reinforcement and nonreinforcement respectively, and hence were relevant to the solution of the discrimination, but X and Y signalled these two outcomes equally, and hence were irrelevant. In the experiments reported here, A and B belonged to one stimulus dimension, and X and Y to another. Experiment 4 (and Experiment 5 to some extent) demonstrated that when stimuli from the initially relevant dimension were relevant in a subsequent transfer discrimination, learning proceeded more readily than when stimuli from the previously irrelevant dimension were relevant. These results were interpreted in terms of Mackintosh's (1975a) theory of attention. That is, it was assumed that during training, attention increased to relevant stimuli as they were the most accurate predictors of the outcome that followed them, facilitating subsequent learning about them. These findings could not be explained in terms of the Rescorla-Wagner (1972) model, or the theory of attention proposed by Pearce and Hall (1980).

It was, however, suggested that rather than appealing to Mackintosh's (1975a) principles, it was possible to explain these results in terms of a peripheral orienting process that directed the eyes towards relevant stimuli because they had been presented in close contiguity with reinforcement during training. The results of Experiment 6 provided evidence against this account, and support for an untested prediction of Mackintosh's theory, by demonstrating that attention increased to relevant stimuli that consistently signalled nonreinforcement during training. Finally,

the results of Experiment 7 provided further evidence that the associability changes observed operate in the manner proposed by Mackintosh, whilst ruling out a number of alternative accounts.

In summary, the experiments reported in this thesis provide evidence that attentional processes limit what is learned about irrelevant stimuli during discrimination learning. However I showed in Chapter 1 that of those theories discussed, no single one is able to account for all of these results as well as related learning phenomena that have been described. The theory of Mackintosh (1975a) appears to be the most successful, but, as described in Chapter 1, it also has its shortcomings. In light of these limitations, Le Pelley (2004) combined components from Mackintosh's theory, the Pearce-Hall (1980) model and the Rescorla-Wagner (1972) theory in an attempt to provide the most encompassing explanation of learning phenomena. The following discussion will examine the implications of my results for this hybrid theory.

Le Pelley (2004)

Unlike the theory of Mackintosh (1975a), the Pearce-Hall (1980) model and Rescorla-Wagner (1972) theory contain a summed error term that takes into account the contribution of all stimuli present on a given trial to calculate changes in the associative strength of any one of those stimuli. Le Pelley (2004) incorporates this concept into his hybrid model in the calculation of R , which is defined as the effective strength of the US on a given trial. It is also assumed that if a stimulus is presented in the absence of the US, it will form an association with a "no-US" representation. Therefore, in Equation 6.1, the term in parentheses represents the discrepancy between the total associative strength of all CS-US (ΣV) connections, and the total

associative strength of all CS-“no-US” connections ($\Sigma \bar{V}$) to give the net associative strength for the cues presented. This value is compared to the total associative strength supported by the US (λ) to give R.

$$R = \lambda - (\Sigma V - \Sigma \bar{V}) \quad (6.1)$$

If this value is positive, then there is a positive discrepancy between the total associative strength supportable by the US and that predicted by the cues present, that is, the magnitude of the reinforcer is underestimated. In this case learning will be excitatory, and changes in the associative strength of a given cue, A, will proceed according to Equation 6.2.

$$\Delta V_A = \alpha_A \sigma_A \beta_E \cdot (1 - V_A + \bar{V}_A) \cdot |R| \quad (6.2)$$

If R is negative, then the magnitude of the reinforcer is overestimated and learning will be inhibitory. In this case the strength of the association between A and “no-US” will be increased according to Equation 6.3.

$$\Delta \bar{V}_A = \alpha_A \sigma_A \beta_I \cdot (1 - \bar{V}_A + V_A) \cdot |R| \quad (6.3)$$

In Equations 6.2 and 6.3, R modulates the amount of learning undergone. For example, a large, positive R value indicates that there is a large discrepancy between the predicted US and the actual US, and thus large increments in associative strength might be expected. The use of the other error term, $1 - V_A + \bar{V}_A$ in Equation 6.2,

and $1 - \bar{V}_A + V_A$ in Equation 6.3, ensures that the net associative strength of each element within a compound, not just the summed effect of the compound, has an effect on the associative change undergone by that element.

In Equations 6.2 and 6.3, α represents Mackintosh's alpha, which determines which stimuli should be attended to. Le Pelley (2004) presents formal equations for calculating the changes in α , the "attentional associability" of a stimulus on a given trial. For the present purposes it is sufficient to acknowledge that, as in the Mackintosh (1975a) model, these equations ensure that attention increases to stimuli that are accurate predictors of the outcome and decreases to stimuli that are inaccurate predictors of the outcome. σ represents the Pearce-Hall (1980) alpha, which, according to Le Pelley determines "salience associability", or how much is learned about a given stimulus. σ is updated according to a modified version of the Pearce-Hall equation that was given in Chapter 1, in order to allow differential weights to be afforded to events occurring on the preceding trial and those occurring before that (Pearce, Kaye and Hall, 1989). However the fundamental assumption that stimuli which are followed by a surprising outcome maintain a high salience associability is the same.

It is assumed that the starting values of α and σ for a novel stimulus are near their maximum, and thus associability effects reflect decreases in the associability of the stimuli involved. Thus the superiority of an IDS group over an EDS group is explained in terms of a decrease in the associability of irrelevant stimuli in the IDS group, which facilitates a novel discrimination when these stimuli are again irrelevant. Finally, the value of α is said to range from 0.05 to 1, whereas σ ranges from 0.5 to 1. The implication of these parameters is that attentional associability potentially has greater importance than salience associability. With reference to Equation 6.2 for

example, learning can effectively be stopped if α is at its lowest level, but the lowest level of σ will not have the same impact.

By incorporating Mackintosh's (1975a) principles, the hybrid theory is able to account for the results reported in this thesis, as well as explaining certain phenomena that pose a problem for the original Mackintosh model. One of these is its inability to account for the phenomenon of conditioned inhibition. That is, the finding that training with A+ AX- endows X with inhibitory properties, such that if X is subsequently conditioned alone, learning will be retarded relative to that if X was a novel stimulus. Mackintosh's model fails to predict this outcome because of the assumption that changes in associative strength are established separately to the individual elements within the compound AX. On the first AX- trial, the associative strength of the novel stimulus X is zero, which is equal to the value of the asymptote on that trial. As a result, there will be no further changes in the associative strength of X during training, and it will fail a summation test for inhibition.

The inclusion of the summed error term to calculate R allows the hybrid model to account for conditioned inhibition. It was stated previously that inhibitory learning occurs when the US is overestimated. Such overestimation might be expected in the conditioned inhibition paradigm, where as a result of A+ trials, the subject is likely to incorrectly predict that the US will follow initial trials of AX-. On an AX- trial, the value of λ will be zero, and as a result of A+ trials the value of $(\Sigma V - \Sigma \bar{V})$ in Equation 6.1 will be positive. The resultant value of R will be negative, and there will be inhibitory learning about both A and X, that is, the strength of the A-"no US" association and X-"no US" association will be increased (although there will also be excitatory learning about A as a result of A+ trials).

The hybrid model also predicts one trial blocking, which is a problematic finding for the Mackintosh (1975a) model. If A is conditioned alone prior to conditioning with AX, on the first AX+ trial, the value of R will be close to zero, as the strength of the A-US association will be close to asymptote, but the X-US, A-no US and X-no US associations will be equal to zero. Thus there will be little learning about X, as well as little more learning about A, from the first trial onwards. Furthermore, from the second trial onwards, the attentional associability of X will decrease as A is a better predictor of reinforcement, and the salience associability of X will decline as this component accurately predicts reinforcement. The hybrid model can also account for those findings discussed in Chapter 1 which suggest that a US processing mechanism, or indeed both a CS and US processing mechanism, is involved in certain demonstrations of blocking and unblocking (e.g. Holland & Fox, 2003; Holland & Kenmuir, 2005).

By including an associability term which represents salience (based on alpha from the Pearce-Hall (1980) model) the hybrid model provides a ready explanation for Hall-Pearce (1979) negative transfer, which the Mackintosh (1975a) model fails to do. A negative transfer experiment can be conceptualised as follows: A → us then A → US, where “us” represents a weak shock, and “US” a strong shock. During initial pairings of A with the weak shock, the salience of A will decline as it becomes an increasingly good predictor of the outcome, but attention to A will increase as it is the best predictor of the outcome. Due to the starting value of A being near its maximum however, this increase will only be slight. When A is paired with the strong US, compared to a group that did not receive pretraining, the salience of A is considerably reduced, but the attentional associability of A is only slightly higher. Thus

conditioned responding will be slower to develop in the group that received the initial training with A and the weak shock.

Despite its efficacy at explaining these learning phenomena, the theory devised by Le Pelley (2004) is unable to account for the results of an experiment reported by George and Pearce (1999). George and Pearce (1999) presented pigeons with the discriminations given in Table 6.1, where A and B represent stimuli from one dimension, W, X, Y and Z represent stimuli from a second dimension, and P and Q represent stimuli from a third dimension. Consider the training given in Stage 1. During this stage, each element is followed by food on 50% of its presentations, thus individually each is a poor predictor of the outcome. However, specific combinations of these elements are accurate predictors of the outcome. That is, AW and BX are consistently reinforced, and BW and AX are consistently nonreinforced. For this reason, the stimuli A, B, W and X can be considered to be relevant, whereas P and Q are irrelevant. After Stage 1, W and X were replaced by two novel stimuli from the same dimension, Y and Z. In Group Relevant, the same dimensions were relevant in Stage 2, so the relevant stimuli were A, B, Y and Z (AY and BZ consistently signalled food, BY and AZ consistently signalled the absence of food). In Group Irrelevant, A and B became irrelevant in Stage 2, such that the relevant stimuli were Y, Z and the stimuli from the previously irrelevant dimension, P and Q. That is, the combination of stimuli YP and ZQ consistently signalled food, and YQ and ZP consistently signalled the absence of food, regardless of whether these compounds were accompanied by A or B.

Table 6.1. Discrimination Training Received in Stages 1 and 2 of Experiment 2, George and Pearce (1999).

Stage 1		Stage 2			
Both Groups		Group Relevant		Group Irrelevant	
AWP+	BWP-	AYP+	BYP-	AYP+	AYQ-
BXP+	AXP-	BZP+	AZP-	AZQ+	AZP-
AWQ+	BWQ-	AYQ+	BYQ-	BYP+	BYQ-
BXQ+	AXQ-	BZQ+	AZQ-	BZQ+	BZP-

Note: Characters in bold represent stimuli that were relevant to the discrimination.

If attention is established to individual stimuli based on how well they predict the outcome, as proposed by Mackintosh (1975a) and Le Pelley (2004), then there should be no difference in the amount of attention paid to any of the stimuli during training because all were followed by the outcome on 50% of presentations. Thus Group Relevant and Group Irrelevant would be expected to acquire the discrimination in Stage 2 at a comparable rate. However, George and Pearce (1999) found that Group Relevant acquired the discrimination in Stage 2 more quickly than Group Irrelevant. This finding can be explained if it is assumed that attention increased to the relevant combinations of stimuli presented during Stage 1. If this were the case then the training given in Stage 1 would result in greater attention being paid to A and B than to P and Q during Stage 2. Such a change in attention should facilitate acquisition of the discrimination in Stage 2 for Group Relevant, when A and B are again relevant, but should hinder Group Irrelevant, as these stimuli become irrelevant.

The hybrid model proposed by Le Pelley (2004) is unable to explain how biconditional discriminations such as these are solved. In order for the Rescorla-Wagner (1972) model to explain discriminations of this kind, Wagner and Rescorla

(1972) suggested that when two stimuli are presented together, they create a unique configural cue which can enter into associations in the same way as A and B.

Consider the discrimination A+ B+ AB-. If it is assumed that responding to the compound AB is determined purely by the sum of the associative strengths of A and B, then this discrimination will not be solved. However, if AB is represented by ABX, where X is a configural cue, as training progresses, X will gain inhibitory properties due to the high associative strengths of A and B. As a result, the overall associative strength of the compound will fall and eventually it will elicit little responding.

Even if this concept is adopted by the hybrid model proposed by Le Pelley (2004), it still fails to account for the results of George and Pearce (1999). If each of the compounds presented has a configural cue, then this cue will be the best predictor of the outcome. As a result the configural cue will gain associability at the expense of other stimuli within the compound, and subsequent learning about stimuli that are otherwise relevant will not be facilitated. However, another hybrid model, proposed by Pearce, George and Redhead (1998) is able to account for the findings of George and Pearce.

Pearce, George and Redhead (1998)

The theories described thus far assume that when an animal is presented with a compound stimulus such as AWP+, each of the elements that comprise the compound (A, W and P) enters into a separate association with the US. The model proposed by Pearce et al. (1998) is derived from the configural theory of Pearce (1987, 1994), which assumes that the entire pattern of stimulation, AWP, will enter into a single association with the US. Pearce et al. (1998) extended this theory by including an attentional mechanism based on that proposed by Mackintosh (1975a). A schematic

diagram of the connectionist network based on that proposed by Pearce (1994) is presented in Figure 3, which includes a layer of input units, activated by individual stimuli, and a layer of configural units, which represent combinations of these stimuli. The figure shows the configural units that are formed during Stage 1 of the George and Pearce (1999) experiment detailed in Table 6.1, and the connections that will develop when an AWP+ trial is presented.

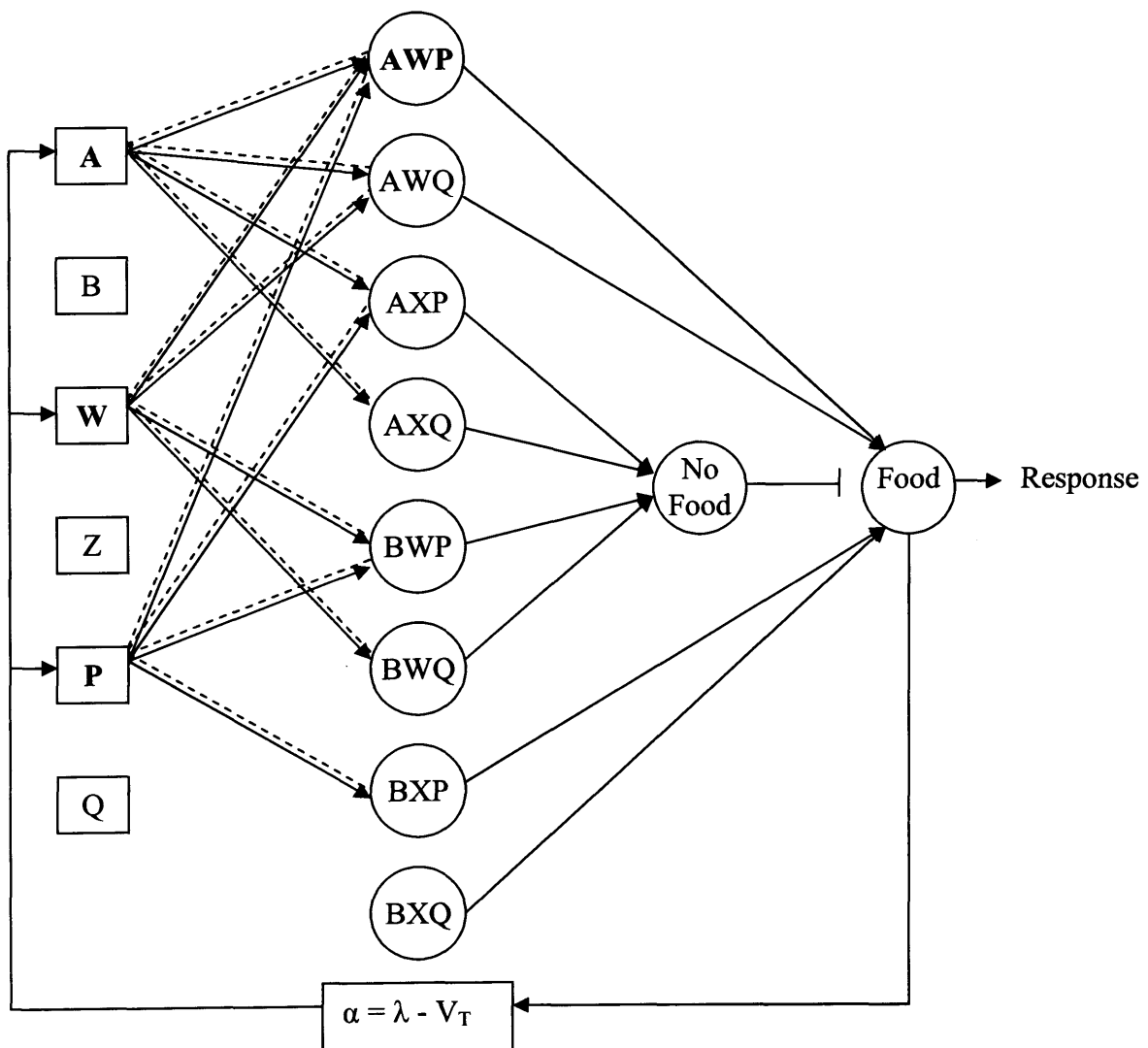


Figure 6.2. The connections formed in a configural connectionist network during Stage 1 of George and Pearce (1999) Experiment 2. The dashed lines represent feedback from the configural units back to the active input units.

The first layer of the model contains input units, one for each of the individual stimuli involved in the discrimination. According to the model, presentation of the stimulus AWP will activate the input units A, W and P, which in turn will each fully activate the configural unit AWP that represents the combined presence of these stimuli. Some configural units will be activated quite strongly by two input units (for example, AWQ), others will be weakly activated by one input unit (for example, AXQ), and just one will not be activated (BXQ). Half of the configural units correspond to compounds that signal food, and these will activate the output unit 'Food' to an extent determined by their own level of activation. The remaining configural units correspond to compounds that were nonreinforced, and these will inhibit activation of the Food output unit to an amount determined by their level of activation.

The dashed lines represent activation that is fed back to the input units from the configural units, allowing the extent to which a configural unit accurately predicts the outcome of a trial to influence the extent to which the input units are activated. The value of the signal fed back is positive if the configural unit predicts the correct outcome, and negative if it predicts the incorrect outcome, thereby ensuring that stimuli that are relevant to the discrimination will receive more activation than irrelevant stimuli. Consider the feedback that propagates from the configural units to input unit A, which represents a stimulus that was relevant during Stage 1, when subjects receive a reinforced presentation of AWP. Each of the input units representing the stimuli A, W and P is activated, and all three of these units activate the configural unit AWP. Pearce et al. (1998) represent the level of feedback from this configural unit to the input unit A as +1, where the plus indicates that the AWP unit

that has been activated predicts the correct outcome of an AWP trial (food), and 1 represents the fact that all input units connected to the AWP unit are active.

Presentation of the AWP compound also activates an AWQ configural unit, via the input units A and W. This unit is also connected to the food unit, and therefore correctly predicts the outcome of an AWP trial, meaning that the feedback to the input unit A will be positive. However, only two of the three input units activate the AWQ unit, and therefore the value of the feedback to the unit A in this case will be $+.66$. Following this reasoning, the value of the feedback from AXP to A will be $-.66$, as this configural unit predicts the incorrect outcome. The value of the feedback from AXQ will be $-.33$ as only A activates this unit and it also predicts the incorrect outcome. The sum of these four values is $.66$. Now consider the feedback that proceeds from the configural units to input unit P, which represents a stimulus that was irrelevant during Stage 1, when subjects receive a reinforced presentation of AWP. Unit P will receive feedback from the units AWP, AXP, BWP and BXP, with the values of $+1$, $-.66$, $-.66$ and $.33$ respectively, the sum of these four values being 0.

Thus when AWP is presented, the input unit A, which represents a relevant stimulus, will receive greater activation than input unit P, which represents an irrelevant stimulus. As a consequence, the effective salience of P will be reduced relative to that of A. Thus by adjusting the level of activation of the input units via feedback from the configural units, it will be possible for the network to pay more attention to relevant than to irrelevant stimuli. This change in attention will aid the discrimination by increasing generalisation among compounds that signal the same outcome and decreasing generalisation among compounds that signal different outcomes. For example, due to the extra attention received by A and W, there will be more generalisation between AWP and AWQ (which both signal food) than there will

be between AWP and AXP (the latter of which signals no food) as AWP and AWQ have two elements in common, but due to the low salience of P, AWP and AXP effectively have just one element in common.

This mechanism represents Mackintosh's (1975a) alpha, and cannot account for effects such as Pearce-Hall negative transfer. Thus, the Pearce-Hall (1980) alpha (determined by the discrepancy $\lambda - V_T$) is also incorporated into the model, via a loop that feeds back from the US representation to the input layer. If this value is high, the input units activated inaccurately predict the outcome and will all be strongly activated on a subsequent trial. If the value of this term is low, the input units accurately predict the outcome and will subsequently be only weakly activated. Thus when subjects have learned that AWP leads to food, the salience of these stimuli will be decreased by the Pearce-Hall term. However, the Mackintosh mechanism ensures that during a new discrimination, more attention will be paid to A and W than to P.

Future Directions

The critical conclusion from this thesis is that for any model to provide a comprehensive account for discrimination learning, it firstly will be based on the assumption that little is learned about irrelevant stimuli, and secondly must include a mechanism for enabling changes in attention to occur during discrimination learning. I shall now discuss how future research might elaborate on these conclusions.

Testing the comparator hypothesis

Chapter 2 provided support for the assumption that little is learned about irrelevant stimuli, contrary to the predictions of the comparator hypothesis. Evidence for the assumption that irrelevant stimuli are learned about normally comes primarily

from demonstrations of retrospective revaluation, but in agreement with a number of other studies (e.g. Holland, 1999; Rauhut et al., 2000) the experiments reported in Chapter 2 failed to produce this effect. Other researchers (e.g. Blaisdell et al., 1999; Liljeholm & Balleine, 2006) have provided support for the comparator hypothesis using similar experiments, but these studies have involved specific training parameters that seem to be required if the effect is to be found. The precise conditions that give rise to retrospective revaluation remain to be determined. However, the predictions of the comparator hypothesis relative to those of the Rescorla-Wagner (1972) model can be tested in other ways that do not rely on retrospective revaluation.

A pilot experiment was conducted in order to test another prediction derived from the comparator hypothesis. Rats were presented with AX+ and BX- trials, where A was a houselight, B was a magazine light and X was white noise. On each of the 26 sessions of training, Group Few received 8 AX+ trials and 8 BX- trials. Group Many received 8 AX+ trials and 64 BX- trials. X was then tested individually. According to the comparator hypothesis, by the end of training the X-US association will be much weaker in Group Many, where it is paired with the US on just 1 in 9 trials, than in Group Few, where it is paired with the US on 1 in 2 trials. It therefore follows from this theory that Group Few will respond more to X on test than Group Many.

According to the Rescorla-Wagner (1972) model, with more BX- trials in Group Many than in Group Few, learning should proceed more readily in the former group. However, at asymptote, the associative strength of X should be the same in both groups. Thus provided that learning has reached asymptote, the Rescorla-Wagner (1972) model predicts that there will be no difference between the two groups at test. In fact, both groups showed minimal responding to X when this stimulus was tested alone, which did not allow the data to be interpreted in a meaningful way. It is

tempting to conclude that this outcome, which is not predicted by either theory, was a consequence of learning about the irrelevant stimulus X being disrupted through a lack of attention. If this interpretation is correct, then these findings present further problems for the comparator hypothesis.

Associability effects in different species

The results from Chapters 3, 4 and 5 provided convincing evidence that pigeons learn little about irrelevant stimuli because they pay little attention to them. Experiment 5 provided some evidence for attentional changes in rats, although the results were not as convincing as those reported for pigeons. In the discussion to Experiment 5, various improvements on the design were suggested to improve its efficacy in rats. In addition to these suggestions, with pigeons the use of the novel combination of stimuli during the test discrimination in Experiment 7 was found to yield similar results to when all compounds were familiar (as in Experiments 4 and 6). Using three familiar compounds on test necessitated the large number of trial types presented during training in Experiment 5, and by making one compound unfamiliar, the number of trial types could be reduced. Such a modification may improve performance on a training discrimination which was clearly difficult for rats to acquire. In Chapter 3, other experiments that have investigated associability changes in rats were described, and it was argued that the results from the majority of these experiments could be explained in terms of acquired equivalence. Such an explanation cannot account for the results observed with pigeons reported in this thesis. Thus a replication of this effect using the same design as that used in Experiment 4 but with rats would support the results of Oswald et al. (2001), which indicate that the acquired equivalence account is not sufficient to explain all associability effects in rats.

Orienting responses

It was suggested that the associability changes observed in Experiment 4 could be explained in terms of a peripheral orienting process that directed gaze towards relevant stimuli because these stimuli were presented in close contiguity with food. This explanation seems unlikely given the results of Experiments 6 and 7, however, it could be argued that these experiments did not entirely rule this account out, as stimuli from the relevant and irrelevant dimensions appeared in different locations. It would therefore be of interest to explicitly test this hypothesis. Such a test could involve the design used in Experiment 4 reported here, but stimuli from the dimension of colour could be replaced with different spatial locations on the TV monitor. Thus in training of the sort AX+ BX- AY+ BY-, AX would represent a pattern presented at location A, BX would represent the same pattern at location B, and so on. This design would ensure that any associability changes could not be the result of subjects learning to orient towards relevant stimuli and away from irrelevant stimuli.

Changes in attention to specific stimuli or to stimulus dimensions

In Chapter 5 it was suggested that changes in attention are established to individual stimuli, and generalise to other stimuli on the basis of similarity. There is in fact little evidence in the literature relating to this issue, and it remains plausible that during simple discrimination learning attention increases to entire dimensions. Subsequent experiments might utilise the design reported in this thesis, but rather than presenting stimuli from two separate dimensions, both relevant and irrelevant stimuli could be from the same dimension. If similar changes in attention to those reported here were observed, it would provide convincing evidence that attention is stimulus-specific.

Pilot work has suggested that this experiment would be successful. The following experiment involved pigeons in a visual search task. A screen was divided into a matrix of 12 touch-sensitive rectangles. Each of these rectangles contained a pattern containing 60 small coloured squares, such that the pattern AX consisted of 30 squares of colour A randomly intermixed with 30 squares of colour X. Within each array there was one target pattern, and 11 identical distractor patterns. Pecking the target pattern resulted in the delivery of food. Pecks to any of the other 11 patterns presented were nonreinforced. Examples of the trial types given are presented in Table 6.2.

Table 6.2. Example Trial Types Given in a Pilot Visual Search Experiment

Training		Test	
Target	Distractor	Target	Distractor
AX+	BX-	AX+	BX-
AY+	BY-	BY+	BX-
BX+	AX-		
BY+	AY-		

During training, the colours A and B were relevant to solving the discrimination, and the colours X and Y were irrelevant. That is, on each trial type the colours that distinguished the correct target pattern from the incorrect distractor patterns were the colours A and B. Following training, test trial types of the kind presented in Table 6.2 were given. For trials on which the target was AX and the distractors were BX, the colours that had previously been relevant during training were again relevant, and subjects accurately located the target pattern. However, on trials when the target was BY and the distractors BX, the previously irrelevant colours

X and Y were relevant and subjects were significantly less accurate at locating the target. These results were taken as evidence that attention increased to relevant colours and decreased to irrelevant colours during training. However it is possible that in learning to peck the “odd one out”, pigeons learned to peck A and B and avoid pecking X and Y. Thus when A or B was the target they would respond accurately, but when X or Y was the target, they would be reluctant to peck the correct pattern. It is difficult to think of a test that would rule out this alternative interpretation, but the results suggest that a replication of Experiment 4, say, with some colours serving as the relevant stimuli, and others as the irrelevant stimuli, would again reveal that the associability of the relevant stimuli was greater than that of the irrelevant stimuli.

Testing the Pearce-Hall (1980) account

Finally, the stimuli used in Experiments 4, 6 and 7 could be used to test the prediction of the Pearce-Hall (1980) model that attention increases to stimuli that are poor predictors of the outcome. Consider the discrimination $A^+ B^+ X+/- Y+/-$. In this discrimination, A and B are accurate predictors of reinforcement, and X and Y are less accurate predictors of the outcome that follows them as they are only partially reinforced. According to the Pearce-Hall account, this treatment should result in more attention being paid to X and Y than to A and B. Thus following the training discrimination, a group that receives the discrimination $AX^+ AY^-$, for which X and Y are relevant, should acquire their discrimination more readily than a group that receives the discrimination $AX^+ BX^-$, for which A and B are relevant. In contrast, it follows from the theory of Mackintosh (1975a) that attention should increase to A and B during training at the expense of X and Y, and hence the opposite pattern of results is predicted. An unpublished experiment conducted by Esber in our laboratory has

confirmed the prediction from the Pearce-Hall theory with rats. It is now important to see if this effect can be replicated with pigeons.

General Conclusions

To conclude, the experiments reported in this thesis have provided convincing evidence that animals pay relatively little attention to irrelevant stimuli in their environment, and as a result they learn about them slowly. An attentional mechanism is therefore a vital component of any theory of learning that is to explain the fate of irrelevant stimuli. At present, hybrid models provide the most comprehensive account for these results, but some questions about how attentional processes function remain unanswered. The novel method described in this thesis will provide a useful tool for addressing these questions.

References

- Balaz, M. A., Kasprow, W. J., & Miller, R. R. (1982). Blocking with a single compound trial. *Animal Learning and Behavior*, 10, 271–276.
- Balleine, B. W., Espinet, A., & González, F. (2005). Perceptual learning enhances retrospective revaluation of conditioned flavor preferences in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 31, 341–350.
- Baxter, M. G., Gallagher, M., & Holland, P. C. (1999). Blocking can occur without losses in attention in rats with selective removal of hippocampal cholinergic input. *Behavioral Neuroscience*, 113, 881–890.
- Birrell, J.M., & Brown, V.J. (2000). Medial frontal cortex mediates perceptual attentional set shifting in the rat. *Journal of Neuroscience*, 20, 4320–4324.
- Blaisdell, A. P., Gunther, L. M., & Miller, R. R. (1999). Recovery from blocking achieved by extinguishing the blocking CS. *Animal Learning and Behavior*, 27, 63–76.
- Blaisdell, A. P., & Miller, R. R. (2001). Conditioned inhibition produced by extinction-mediated recovery from the relative stimulus validity effect: A test of acquisition and performance models of empirical retrospective revaluation. *Journal of Experimental Psychology: Animal Behavior Processes*, 27, 48–58.
- Blanchard, R. (1975). The effect of S- on observing behaviour. *Learning and Motivation*, 6, 1–10.
- Cardinal, R.N. (2000). *Whisker*, version 1.0, computer software. URL: <http://www.whiskercontrol.com>.
- Cole, R. P., Barnet, R. C., & Miller, R. R. (1995). Effect of relative stimulus validity:

- Learning or performance deficit? *Journal of Experimental Psychology: Animal Behavior Processes*, 21, 293-303.
- Couvillon, P. A., Tennant, W. A., & Bitterman, M. E. (1976). Intradimensional vs. Extradimensional transfer in the discriminative learning of goldfish and pigeons. *Animal Learning and Behavior*, 4, 197-203.
- Denniston, J. C., Savastano, H. I., & Miller, R. R. (2001). The extended comparator hypothesis: Learning by contiguity, responding by relative strength. In R. R. Mowrer & S. B. Klein (Eds.), *Handbook of contemporary learning theories* (pp. 65-117). Hillsdale, NJ: Erlbaum.
- Dias, R., Robbins, T. W., & Roberts, A. C. (1996). Dissociation of affective and attentional shifting by selective lesions of prefrontal cortex. *Nature*, 380, 69-72.
- Dickinson, A., & Burke, J. (1996). Within-compound associations mediate the retrospective revaluation of causality judgements. *Quarterly Journal of Experimental Psychology*, 49B, 60-80.
- Dickinson, A., Hall, G., & Mackintosh, N. J. (1976). Surprise and the attenuation of blocking. *Journal of Experimental Psychology: Animal Behavior Processes*, 2, 313-322.
- Dickinson, A., Nicholas, D. J., & Mackintosh, N. J. (1983). A re-examination of one-trial blocking in conditioned suppression. *Quarterly Journal of Experimental Psychology*, 35B, 67-79.
- Duffaud, A.M., Killcross, S., & George, D.N. (2007). Optional-shift behaviour in rats: A novel procedure for assessing attentional processes in discrimination learning. *Quarterly Journal of Experimental Psychology*, 60, 534-542.
- Esber, G.R., Pearce, J.M., & Haselgrove, M. (in press). Enhancement of responding to

- A following A+ / AX+ training: Challenges for a comparator theory of learning. *Journal of Experimental Psychology: Animal Behavior Processes*.
- George, D. N., & Pearce, J. M. (1999). Acquired distinctiveness is controlled by stimulus relevance not correlation with reward. *Journal of Experimental Psychology: Animal Behavior Processes*, 25, 363–373.
- Gibson, E.J. (1940). A systematic application of the concepts of generalization and differentiation to verbal learning. *Psychological Review*, 47, 196-229.
- Hall, G. (1991). *Perceptual and associative learning*. Oxford: Oxford University Press.
- Hall, G., & Channell, S. (1985). A comparison of intradimensional and extradimensional shift learning in pigeons. *Behaviour Processes*, 10, 285-295.
- Hall, G., & Pearce, J. M. (1979). Latent inhibition of a CS during CS–US pairings. *Journal of Experimental Psychology: Animal Behavior Processes*, 3, 31–42.
- Hall, G., & Pearce, J. M. (1982). Restoring the associability of a pre-exposed CS by a surprising event. *Quarterly Journal of Experimental Psychology*, 34B, 127–140.
- Hearst, E., & Franklin, S.R. (1977). Positive and negative relations between a signal and food – approach-withdrawal behaviour to signal. *Journal of Experimental Psychology: Animal Behavior Processes*, 3, 37-52.
- Holland, P.C. (1977). Conditioned stimulus as a determinant of the form of the Pavlovian conditioned response. *Journal of Experimental Psychology: Animal Behavior Processes*, 3, 77-104.
- Holland, P. C. (1985). Pretraining a compound conditioned stimulus reduces unblocking. *Bulletin of the Psychonomic Society*, 23, 237–240.

- Holland, P. C. (1999). Overshadowing and blocking as acquisition deficits: No recovery after extinction of overshadowing or blocking cues. *Quarterly Journal of Experimental Psychology*, 52B, 307-333.
- Holland, P. C., & Fox, G. D. (2003). Effects of hippocampal lesions in overshadowing and blocking procedures. *Behavioral Neuroscience*, 117, 650–656.
- Holland, P. C., & Gallagher, M. (1993a). Effects of amygdala central nucleus lesions on blocking and unblocking. *Behavioral Neuroscience*, 107, 235–245.
- Holland, P. C., & Gallagher, M. (1993b). Amygdala central nucleus lesions disrupt increments, but not decrements, in CS processing. *Behavioral Neuroscience*, 107, 246–253.
- Holland, P. C., & Kenmuir, C. (2005). Variations in unconditioned stimulus processing in unblocking. *Journal of Experimental Psychology: Animal Behavior Processes*, 31, 155-171.
- Honey, R.C., & Hall, G. (1989). Acquired equivalence and distinctiveness of cues. *Journal of Experimental Psychology: Animal Behavior Processes*, 16, 178-184.
- Kamin, L. J. (1969). Selective association and conditioning. In N. J. Mackintosh & W. K. Honig (Eds.), *Fundamental Issues in Associative Learning* (pp. 42-64). Halifax: Dalhousie University Press.
- Kaufman, M. A., & Bolles, R. C. (1981). A nonassociative aspect of overshadowing. *Bulletin of the Psychonomic Society*, 18, 318-320.
- Kaye, H., & Pearce, J. M. (1987). Hippocampal lesions attenuate latent inhibition and the decline of the orienting response in rats. *Quarterly Journal of Experimental Psychology*, 39B, 107–125.

- Kaye, H., & Pearce. (1984). The strength of the orienting response during Pavlovian conditioning. *Journal of Experimental Psychology: Animal Behavior Processes*, 10, 90-109.
- Kirk, R.E. (1968). *Experimental Design : Procedures for the Behavioural Sciences*. Belmont, CA: Brooks/Cole.
- Le Pelley, M. E. (2004). The role of associative history in models of associative learning: A selective review and a hybrid model. *Quarterly Review of Experimental Psychology: Comparative and Physiological Psychology*, 57(B), 193–243.
- Lieberman, D.A. (1972). Secondary reinforcement and information as determinants of observing behaviour in monkeys (*macaca mulatta*). *Learning and Motivation*, 3, 341-358.
- Liljeholm, M., & Balleine, B. W. (2006). Stimulus salience and retrospective revaluation. *Journal of Experimental Psychology: Animal Behavior Processes*, 32, 481-487.
- Mackintosh, N. J. (1974). *The Psychology of Animal Learning*. London: Academic Press.
- Mackintosh, N. J. (1975a). A theory of attention: Variations in the associability of stimuli with reinforcement. *Psychological Review*, 82, 276– 298.
- Mackintosh, N. J. (1975b). Blocking of conditioned suppression: Role of the first compound trial. *Journal of Experimental Psychology: Animal Behavior Processes*, 1, 335-345.
- Mackintosh, N. J., & Little, L. (1969). Intradimensional and extradimensional shift learning by pigeons. *Psychonomic Science*, 14, 5–6.
- Mackintosh, N. J., & Turner, C. (1971). Blocking as a function of novelty of CS and

predictability of UCS. *Quarterly Journal of Experimental Psychology*, 23, 359–366.

Matzel, L. D., Schachtman, T. R., & Miller, R. R. (1985). Recovery of an overshadowed association achieved by extinction of the overshadowing stimulus. *Learning and Motivation*, 16, 398-412.

Matzel, L. D., Shuster, K., & Miller, R. R. (1987). Covariation in conditioned response strength between stimuli trained in compound. *Animal Learning and Behavior*, 15, 439-447.

Melchers, K. G., Lachnit, H., & Shanks, D. R. (2006). The comparator theory fails to account for the selective role of within-compound associations in cue-selection effects. *Experimental Psychology*, 53, 316-320.

Miller, R. R., Barnet, R. C., & Grahame, N. J. (1992). Responding to a conditioned stimulus depends on the current associative status of other cues present during training of that specific stimulus. *Journal of Experimental Psychology: Animal Behavior Processes*, 18, 251-264.

Miller, R. R., & Matzel, L. D. (1988). The comparator hypothesis: A response rule for the expression of associations. *The Psychology of Learning and Motivation*, 22, 1-92.

Miller, R. R., & Schachtman, T. R. (1985). Conditioning context as an associative baseline: Implications for response generation and the nature of conditioned inhibition. In R. R. Miller & N. E. Spear (Eds.), *Information processing in animals: Conditioned inhibition* (pp. 51-88). Hillsdale, NJ: Lawrence Erlbaum Associates.

Mueller, K.L., & Dinsmoor, J.A. (1984). Testing the reinforcing properties of S-: A

replication of Lieberman's procedure. *Journal of the Experimental Analysis of Behavior*, 41, 17-25.

Murphy, R. A., Baker, A. G., & Fouquet, N. (2001). Relative validity effects with either one or two more valid cues in Pavlovian and instrumental conditioning. *Journal of Experimental Psychology: Animal Behavior Processes*, 27, 59-67.

Oswald, C.J.P., Yee, B.K., Rawlins, J.N.P., Bannerman, D.B., Good, M., & Honey, R.C. (2001). Involvement of the entorhinal cortex in a process of attentional modulation: Evidence from a novel variant of an IDS/EDS procedure. *Behavioral Neuroscience*, 115, 841-849.

Pearce, J. M. (1987). A model of stimulus generalization for Pavlovian conditioning. *Psychological Review*, 94, 61-73.

Pearce, J. M. (1994). Similarity and discrimination: A selective review and a connectionist model. *Psychological Review*, 101, 587-607.

Pearce, J. M., & Hall, G. (1980). A model for Pavlovian learning: Variations in the effectiveness of conditioned but not of unconditioned stimuli. *Psychological Review*, 106, 532-552.

Pearce, J.M., Esber, G.R., George, D.N., & Haselgrove, M. (2008). The nature of discrimination learning in pigeons. *Learning and Behavior*, 36, 188-199.

Pearce, J. M., George, D. N., & Redhead, E. S. (1998). The role of attention in the solution of conditional discriminations. In N. A. Schmajuk & P. C. Holland (Eds.), *Occasion setting: Associative learning and cognition in animals*. Washington, DC: American Psychological Association.

Rauhut, A. S., McPhee, J. E., DiPietro, N. T., & Ayres, J. B. (2000). Conditioned inhibition training of the competing cue after compound conditioning does not reduce cue competition. *Animal Learning and Behavior*, 28, 92-108.

- Rescorla, R. A. (1981). Simultaneous associations. In P. Harzem & M. D. Zeiler (Eds.), *Predictability, correlation, and contiguity* (pp. 47-80). Chichester: Wiley.
- Rescorla, R.A. (1999). Within-subject partial reinforcement extinction effect in autoshaping. *Quarterly Journal of Experimental Psychology*, 52B, 75-87.
- Rescorla, R. A. (2001). Unequal associative changes when excitors and neutral stimuli are conditioned in compound. *Quarterly Journal of Experimental Psychology*, 54B, 53–68.
- Rescorla, R. A., & Colwill, R. M. (1983). Within-compound associations in unblocking. *Journal of Experimental Psychology: Animal Behavior Processes*, 9, 390-400.
- Rescorla, R. A., & Durlach, P. (1981). Within-event learning in Pavlovian conditioning. In N. E. Spear & R. R. Miller (Eds.), *Information processing in animals: Memory mechanisms* (pp. 81-111). Hillsdale, NJ: Lawrence Erlbaum.
- Rescorla, R.A. & Freberg, L. (1978). The extinction of within-compound flavour associations. *Learning and Motivation*, 9, 411-427.
- Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory* (pp. 64-99). New York: Appleton-Century-Crofts.
- Swan, J. A., & Pearce, J. M. (1988). The orienting response as an index of stimulus associability in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 14, 292–301.
- Savastano, H. I., Arcediano, F., Stout, S. C., & Miller, R. R. (2003). Interactions between preexposure and overshadowing: Further analysis of the extended

- comparator hypothesis. *Quarterly Journal of Experimental Psychology*, 56B, 371-395.
- Savastano, H. I., Yin, H., Barnet, R.C., & Miller, R.R. (1998). Temporal coding in Pavlovian conditioning: Hall-Pearce negative transfer. *Quarterly Journal of Experimental Psychology*, 51B, 139-153.
- Shepp, B. E., & Eimas, P.D. (1964). Intradimensional and extradimensional shifts in the rat. *Journal of Comparative and Physiological Psychology*, 57, 357-364.
- Spence, K.W. (1940). Continuous versus non-continuous interpretations of discrimination learning. *Psychological Review*, 47, 271-288.
- Stout, S. C., & Miller, R. R. (2007). Sometimes-competing retrieval (SOCR): A formalization of the comparator hypothesis. *Psychological Review*, 114, 759-783.
- Sutherland, N. S., & Andelman, L. (1969). Effects of overtraining on intra- and extradimensional shifts. *Psychonomic Science*, 15, 253-354.
- Sutherland, N. S., & Mackintosh, N. J. (1971). *Mechanisms of animal discrimination learning*. New York: Academic Press.
- Trobalon, J. B., Miguelez, D., McLaren, I. P. L., & Mackintosh, N. J. (2003). Intradimensional and extradimensional shifts in spatial learning. *Journal of Experimental Psychology: Animal Behavior Processes*, 29, 143-152.
- Van Hamme, L. J., & Wasserman, E. A. (1994). Cue competition in causality judgements: The role of nonpresentation of compound stimulus elements. *Learning and Motivation*, 25, 127-151.
- Wagner, A. R. (1981). SOP: A model of automatic memory processing in animal behavior. In N. E. Spear & R. R. Miller (Eds.), *Information processing in animals: Memory mechanisms* (pp. 5-47). Hillsdale, N.J.: Erlbaum.

- Wagner, A. R., Logan, F. A., Haberlandt, K., & Price, T. (1968). Stimulus selection in animal discrimination learning. *Journal of Experimental Psychology*, 76, 171-180.
- Wagner, A.R., & Rescorla, R.A. (1972). Inhibition in Pavlovian conditioning: application of a theory. In R.A. Boakes and M.S. Halliday (Eds.), *Information processing in animals: Conditioned inhibition* (pp. 301-336). London: Academic Press.
- Whitney, L., & White, K.G. (1993). Dimensional shift and the transfer of attention. *The Quarterly Journal of Experimental Psychology*, 46B, 225-252.
- Wyckoff, L.B. (1952). The role of observing responses in discrimination learning: Part 1. *Psychological Review*, 59, 431-442.

